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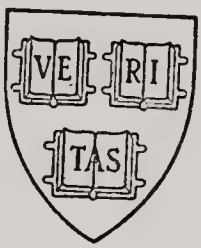

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THE GENERA OF THE SPIDER FAMILY THERIDIIDAE

BY HERBERT W. and LORNA R. LEVI

WITH FOURTEEN PLATES

CAMBRIDGE, MASS., U.S.A.
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AT HARVARD COLLEGE
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THE GENERA OF THE SPIDER FAMILY THERIDIIDAE

By Herbert W. and Lorna R. Levi

With Fourteen Plates

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No. 1 — *The Genera of the Spider Family Theridiidae*

By Herbert W. and Lorna R. Levi

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INTRODUCTION

Of the 140 theridiid genera only about twenty, those with representatives in North America and Europe, and a few whose members are common tropical species, are generally known.

Many of the less known genera were established during the 19th century, when the arrangement of eyes was considered to be of generic importance. This very unfortunate choice of character resulted in a system that, in theridiid spiders (and possibly in some other families), does not reflect natural relationships; indeed, individuals of many species may be variable in regard to the position of the eyes (Levi, 1960a). Furthermore, by present standards, many type species were inadequately described and some were not illustrated. Consequently, later zoologists found it easier to make new genera than to place their species correctly in established genera.

Unlike the species, the genus is a relatively arbitrary taxonomic category. It is a collective category and as such should contain more than one species. Optimum size for genera may be controversial and is probably different for each genus. Experience in other animal groups as well as in spiders has demonstrated that a system of few large genera is more workable than one of innumerable small genera. It is difficult, for instance, to place species in the many closely related genera of the family Salticidae, genera separated in many cases by artificial characters. Well-known cosmopolitan species have been placed in different genera and described as new by various arachnologists. The erigonid (Linyphiidae) genera are based on more natural

characters, but as species only slightly outnumber genera of erigonids, the value of the larger category is lost. Because the limits of the genera have become extremely narrow, placement of new species in so fragmented a family is virtually impossible except by establishment of still more genera. Not only description and placement of new species, and sorting of collections in museums, but also the studies of ecology, behavior, and evolution are made difficult by numerous small genera. To us it appears that a large genus, even one containing several hundred species, is preferable to the many small monotypic genera that would result from breaking up genera like *Theridion* and *Argyrodes*. In case of doubt, a new species should be placed in the closest established genus, rather than in a new monotypic one. Since relationships between species or species groups is unlimited, phylogeny can never be adequately reflected in simple categories like genera, regardless of size. It is assumed, of course, that genera are monophyletic. Further discussion of the nature of higher categories can be found in Mayr (1942, pp. 280-291), Mayr et al. (1953, Chapter 3), and Simpson (1961, pp. 135-140). Problems in determining phylogeny are discussed in Hennig (1950).

At present we know probably less than ten percent of the theridiid fauna. Only the faunas of northern Europe (Wiehle, 1937; Tullgren, 1949; Locket and Millidge, 1953) and America north of Mexico (Kaston, 1946; Levi, 1953-1960; Exline and Levi, 1962) are well known. (These papers, however, include some species found in South and Central America, and other papers on species south of the United States are in manuscript. Many of the Panamanian *Dipoena* described by Chickering in 1943 and 1948 are widespread South American species.) This paper must, therefore, be considered preliminary and will have to be revised after the total fauna is known. It is hoped, however, that the key and new generic diagnoses will encourage others to work up the faunas yet to be described. A conservative treatment of genera makes possible the placement of new species without establishing a new genus for each. Several authors have emphasized the need for gaps between genera, a view we do not share. Many theridiid genera intergrade. Furthermore, we anticipate that extinct species, rediscovered as fossils, might very well bridge gaps between present day genera. Nevertheless, most species fit well within generic limits, and relatively few species fit equally into either of two related genera. The definition of theridiid genera is complicated by the tendency of genera

to run into each other, making it impossible to group them into subfamilies. An exception may be that *Dipoena* and *Euryopis* seem to represent a separate line of evolution.

Travel to study types was made possible by a grant from the National Science Foundation (G-4317); a National Institutes of Health Grant (E-1944) made possible completion of the paper and publication. We are indebted to the following for hospitality at their institutions: Prof. M. Vachon, Muséum National d'Histoire Naturelle, Paris; Dr. E. Tortonese, Museo Civico di Storia Naturale, Genova; Dr. Baldasseroni, Zoological Institute, University of Florence; Dr. M. Beier and Dr. E. Kritscher, Naturhistorisches Museum, Wien; Dr. O. Kraus, Senckenberg Museum, Frankfurt; Dr. G. Owen Evans, Mr. E. Browning, and Mr. K. Hyatt, British Museum (Natural History); Prof. G. C. Varley, Hope Department of Entomology, Oxford University; Dr. L. Brundin, Naturhistoriska Riksmuseet, Stockholm. Prof. P. Zangheri of Parma made a special trip to Florence bringing with him specimens from his collection. The following sent us valuable specimens for examination: Prof. P. Drenski, Zoological Institute, and Dr. N. Atanassov, Naturhistorisches Museum, Bulgarian Academy of Sciences, Sofia; Dr. R. Forster, Otago Museum, Dunedin; Prof. T. Jaczewski, A. Riedel and J. Prószyński, Institute of Zoology, Polish Academy of Sciences, Warsaw; Mr. T. Yaginuma, Osaka; Prof. V. V. Hickman, University of Tasmania; and Dr. M. Birabén, Museum of La Plata. Prof. V. V. Hickman patiently raised *Ancocoelus livens* Simon for us making the study of adult males possible. Several European colleagues, particularly Prof. A. Kaestner, gave us suggestions for this study during discussions at the time of our visit. Dr. B. J. Kaston, Dr. R. Forster, Mrs. D. L. Frizzell (Dr. H. Exline) and Dr. O. Kraus read the manuscript and made valuable suggestions for its improvement.

Familial characters. Although fifty years ago it may have been easy to delimit the family Theridiidae, the recent discovery of numerous species intermediate between it and the related families Linyphiidae, Argiopidae, and Symphytognathidae, has obscured the limits of all these families. While discovery of these intermediate species has made a stimulating contribution to our knowledge of phylogeny, it has at the same time complicated the problem of defining higher taxonomic categories (Table 1).

One of the best and longest known theridiid familial characters, the comb on the fourth tarsus (Fig. 5), may be lacking (e.g. *Pholcomma,* some *Dipoena, Helvibis,* some *Argyrodes,* Fig. 6).

On the other hand, it may be present in members of the family Nesticidae. Although theridiids generally have a characteristic appearance, individual species may bridge the gap between related families. *Pocabletes coroniger* Simon [= *Graphomoa theridioides* Chamberlin], for instance, has many theridiid characters, although it is rightly placed in the Linyphiidae. Generally, in the Theridiidae, the paracymbium is a hook in the alveolus (Figs. 74, 216) or on the distal margin (Figs. 51, 245) of the cymbium of the male palpus, never on the base as in Argiopidae or Nesticidae, or a separate structure as in Linyphiidae. The palpus of Symphytognathidae is (probably secondarily) simple. The labium is usually not rebordered (swollen at the distal end) in Theridiidae, and there may be a seam between it and the sternum. Chelicerae are small, weak, and have a frontal, basal extension (Figs. 10, 13, 15, 17, 19, 21) hidden by the clypeus and only rarely absent (Fig. 12); cheliceral teeth are absent or few in number (rarely more than two, never more than four on the anterior margin, none or rarely one tooth or several minute denticles on the posterior margin). Teeth are borne on the ventral surface (Figs. 9-22). Linyphiid and argiopid spiders have the labium rebordered, have many teeth on both margins of the chelicerae, the chelicerae are stronger, lack of basal extension, and the tooth-bearing surface gently curves medially (Figs. 23-28). The majority of the theridiids lack a colulus (Fig. 1) or have it replaced by two setae (Fig. 2) (exceptions are *Argyrodes, Steatoda, Latrodectus, Robertus,* and *Crustulina*, Figs. 3, 4), while in Nesticidae, Linyphiidae, Argiopidae, Mimetidae and Theridiosomatidae the colulus is always large. Symphytognathidae usually have a large colulus; sometimes it is missing.

The theridiid web is irregular. Viscid threads around the periphery or toward the substratum break when an insect becomes entangled, and pull the insect toward the center of the web (Wiehle, 1931; Nielsen, 1931).

Generic characters. Genitalia prove reliable not only as specific characters but also as phylogenetic clues. Several non-genitalic characters correlate with the structure of the genitalia. In Theridiidae these include size of the colulus (Figs. 1-4) and, to some extent, number of teeth on the margins of the chelicerae (Figs. 9-22) (Levi, 1961). Cheliceral teeth, however, are expected to show some individual variability. In *Dipoena* and *Euryopis* the fangs of the chelicerae are very long and flat (Figs. 9-12), possibly a modification for catching ants.

TABLE 1. Diagnostic features of families close to Theridiidae.

	Theridiidae	Nesticidae	Symphytognathidae	Theridiosomatidae	Argiopidae	Linyphiidae
Chelicerae	no teeth or 1-3 teeth on promargin, rarely 1-3 teeth or denticles on retromargin	few teeth	many small teeth	many teeth	many teeth	many teeth
Labium	usually not swollen distally (rebordered) seam between labium and sternum	swollen distally seam	swollen distally seam	swollen distally seam	swollen distally seam (*Meta*) or free (*Araneus*)	swollen distally seam
Comb on tarsus IV	present, rarely absent	present	sometimes present	no comb	no comb	no comb
Colulus	absent replaced by 2 setae or large	large	large, sometimes absent	large	large	large
Attachment of palpal bulb in alveolus of cymbium	usually at proximal end of alveolus	in center of alveolus	in center of alveolus	in center of alveolus	in center of alveolus	in center of alveolus
Paracymbium	distal end of cymbium, behind bulb or on ectal margin	proximal end of cymbium on ectal margin	probably absent, or on middle of ectal margin	proximal end of cymbium on ectal margin	proximal end of cymbium on ectal margin	a separate sclerite

Eye size and arrangement, characters used by E. Simon and his contemporaries, appear to be unreliable, often varying within species (Levi, 1960a). Although Simon recognized the artificiality of a system based mainly on eye arrangements, some modern authors have used it as an infallible single character. On the other hand, several genera do have constant differences in eye arrangement, and these correlate with other characters. For instance, the lateral eyes are more separated in *Episinus* and *Latrodectus* than in other genera, and in *Episinus* the eyes may be on tubercles. The eyes of *Stemmops* (Fig. 188) and *Coscinida* (Figs. 144, 145) are large and close together.

Eye arrangement may reflect the shape of the carapace, a more important character and one harder to describe. The carapace of males of *Thymoites* is usually modified, although differently in different species (sometimes it is drawn out into an anterior turret bearing anterior median eyes; sometimes it has a groove in the clypeus) (Figs. 121-124, 132). The palpal structure of such males indicates close relationship. Although not closely related (judging by the presence of colulus, cheliceral structure and shape of abdomen), *Argyrodes* males may also have the anterior end of the carapace projecting. The clypeus may have a parallel projection or a seam (Figs. 299, 301). *Dipoena* has a characteristic carapace (Figs. 44-47) often reflected in the position and large size of the anterior median eyes; however, in many species of *Dipoena* the anterior median eyes are equal in size to the other eyes. Of 17 American species of *Dipoena* chosen at random, 9 had anterior median eyes larger than the other eyes, 8 had the anterior median eyes equal in size to the others (the large anterior median eyes are supposed to constitute a diagnostic feature of the genus!). The situation is similar in *Steatoda* (Levi, 1960a).

Although *Episinus* (Fig. 220) and *Anelosimus* (Fig. 184) generally have the carapace longer than in other genera, individual species may have the carapace relatively round. The ratio of carapace length to width varies in *Anelosimus* from 1.2 [*A. aulicum* (C. L. Koch)] to 2.5 [*A. chickeringi* Levi]; in *Episinus* from 1 [*E. panamensis* Levi] to 1.85 [*E. gratiosus* Bryant].

The thoracic groove is rarely of generic importance. There is generally no groove in the carapace of *Robertus*, but *R. vigerens* (Chamberlin and Ivie) has a long longitudinal groove, and

R. laticeps (Keyserling) a depression. A longitudinal depression is common in *Episinus*, but is not present in all species. The shape of the clypeus may be quite variable, even in closely related species (Figs. 44, 47; 123, 124; 299, 301). The labium in closely related species may be almost separated from the sternum (*Dipoena buccalis* Keyserling), or almost no seam may be visible between the two (*Dipoena atlantica* Chickering). Some of these characters, of course, may show individual variation that can be studied only in large series.

The relationship between length of eye region and length of carapace varies in different genera but can not be used as an absolute character, since there are many exceptions. The eye region is shortest in *Anelosimus* (Fig. 184) and some *Episinus* (Figs. 220, 221) and takes a relatively large proportion of the carapace in many *Dipoena* species (Fig. 46).

It is of interest that similar modification of the abdomen often reflects the same close relationship revealed by the genitalia (*Episinus,* Figs. 220, 221, 228; *Achaearanea,* Figs. 79-81; *Phoroncidia,* Figs. 235, 244, 247). Although hard to define, the degree of sclerotization is of generic importance (*Phoroncidia*). A heavily sclerotized spider may have an abdominal scutum, a sclerotized ring around the pedicel, or a sclerotized ring around the spinnerets. Heavy sclerotization is more likely to occur in small theridiids (or in those having a large colulus). However, heavy sclerotization occurs in many genera unrelated by genitalic characters, and may occur in individual species belonging to groups otherwise lightly sclerotized (*Styposis, Pholcomma*).

Relative proportions of leg length is another character unreliable for theridiid classification. Males and females usually have different leg proportions. While in females, the fourth leg is next to longest, usually the second leg is next to longest in males (*Theridion*). The first leg is longest in most genera. In *Stemmops, Euryopis, Theonoe* and *Phoroncidia*, the fourth leg is longest. In many genera, however, different species may have either the fourth or the first leg longest (*Chrosiothes, Dipoena, Enoplognatha, Pholcomma, Thymoites* and *Steatoda*). Often in one sex the first leg is longest, in the other, the fourth, for instance: *Chrosiothes tonala* (Levi), *Chrosiothes goodnightorum* (Levi), *Crustulina altera* Gertsch and Archer, *Enoplognatha joshua* Chamberlin and Ivie, and several *Thymoites* species. Often there is individual variation, so that either the first or fourth is longest (some *Steatoda* species). In general, smaller theridiids have proportionately shorter legs than larger species.

The shortest legs are found in the smallest species (as seen in *Comaroma, Theonoe, Pholcomma*), presumably, those living in litter; the longest legs are found in larger species (*Argyrodes, Chrysso* species), living in webs on vegetation. Leg length often shows geographical variation. In *Latrodectus mactans* (Fabricius) the first patella-tibia is 1.5 to 2.1 times the length of the carapace depending on the part of the range. Nevertheless, there is a superficial taxonomic relationship in leg length, showing many exceptions. In *Anelosimus* the first patella-tibia is 1.3 to 1.9 times the carapace length; however, in *A. rapununi* Levi the carapace and patella-tibia are of equal length. *Dipoena* has relatively short legs, the longest patella-tibia being 1 to 1.4 times the carapace length. In *D. buccalis* Keyserling, however, the male has the first patella-tibia twice the length of the carapace, while in the female it is one and one-half times the carapace length. In *Episinus* this proportion varies from 1.4 to 2.8, in *Chrysso* (admittedly a somewhat heterogeneous assemblage) from 1.2 to 5. Even closely related *Chrysso* species differ widely: 1.2 for the male of *C. mariae* Levi, 2.5 for the male of *C. sulcata* (Keyserling). *Euryopis* is the only genus in which some species have the third leg longer than the second; in all others the third is always shortest. It is of interest that the smallest theridiids generally have the tarsus relatively longer (*Theonoe, Pholcomma* species) than have the larger species. In *Euryopis spinigera* (O.P.-Cambridge) and related species, the tarsi and metatarsi are subequal in length; however in one (undescribed) species the metatarsi are slightly longer than the tarsi in the male and of the same length in the female. (All leg data were taken from the senior author's revision of North American theridiid spiders.) *Argyrodes* species have the middle tarsal claw longer than the lateral claws, possibly an adaptation to their parasitic habit of living in other spiders' webs.

Behavior, particularly web building, undoubtedly encompassing important characters, is relatively little known. Gerhardt (1923, Arch. Naturgesch., vol. 89, p. 64) indicates surprising differences in mating behavior in *Theridion varians* Hahn, on one hand, and *T. tepidariorum* C. L. Koch and *T. formosum* [= *lunatum* (Clerck)], on the other. The latter two species are now considered to belong to *Achaearanea*. However, we do not know whether other species of *Theridion* and *Achaearanea* behave like the species observed, and whether the behavior of *Enoplognatha*

ovata (Clerck) whose behavior was similar to that of *Theridion* (and to linyphiids), is representative of the latter genus.

Unfortunately, the genitalic characters are often difficult to study and, for routine examination, impractical to apply. Often a slight modification of palpal sclerites may give the contracted palpus an appearance entirely different from that of related species. Furthermore, the paleontologist often tries to determine the genus of spiders lacking genitalia, a very difficult if not impossible task.

It has been suggested that genitalic characters be used only to separate species, and that characters other than those of genitalia be used to separate genera. Simpson (1961, p. 145) discusses this point: "It would be a delightful simplification if the characters of organisms had an inherent association with the various categorical ranks. . . . A generic character is one that characterizes a genus, and is not determinable a priori. Identical characters may in one group characterize a species (or even be a mere variation in a species), in another a genus, and in another a family."

Specific characters. Genitalia are usually the reliable characters by which species can be separated. In many genera an examination of the female internal genitalia is essential. Of course, new species (or subspecies) can not be described from juvenile specimens, and for species recognition clear illustrations of the ventral view of the palpus, the epigynum and the internal female genitalia are essential. There are all indications (from the study of North American species) that a large proportion of species are polytypic. This is probably also true in species of other families, but excessive splitting has obscured the variable nature of the species studied.

Despite the importance of genitalic characters, there are examples in the Theridiidae of nongenitalic characters that are of diagnostic importance for species. Although variable, the color and shape of the abdomen of adult female *Dipoena* species are distinct in many species having similar genitalia. The shape of the clypeus of adult males of species related to *Argyrodes caudatus* Taczanowski may be a character easier to observe than small differences in genitalia (Exline and Levi, 1962). There is some indication that in *Helvibis* differences in outline of the carapace constitute a far simpler specific character than slight differences in the very complex genitalia (Levi, in manuscript). But even for the study of these characters mature specimens are necessary.

Type collections. Although the indication of type specimens is established practice today, among 19th century arachnologists it was not. Keyserling did not indicate his types, and as he borrowed large collections from many individuals and institutions, the specimens on which his names are based are now in several different institutions in Europe and America. However, Keyserling kept duplicate specimens in his own collection, later acquired by the British Museum (Natural History). At the turn of the century, Pocock placed type labels into the vials containing species named by Keyserling. This may have been done at the time when all of Keyserling's original labels had to be rewritten because they were becoming faded and illegible. The labels of the Keyserling specimens in the Polish Academy of Sciences have also been rewritten. The type material is not indicated. Many specimens are in poor condition as if they had once been dry. The localities published by Keyserling are sometimes different from the ones on the labels, an error presumably made by Keyserling. Some of Keyserling's specimens in the Naturhistorisches Museum, Vienna, bear Brazilian labels but are actually European species. Keyserling's specimens in Berlin can not be found.

Simon's types are almost all in Paris in excellent care; a few have been lost. Like most of his contemporaries Simon did not indicate types. Often his vials marked with the name of a species contain specimens obviously belonging to several species of similar coloration. There is evidence that Simon put into the same vial all specimens that he considered to belong to a given species, with a single place name indicating the general region from which the specimens were collected. The labels are in clear handwriting on poor grade paper. Luckily most type species were based on single specimens so no lectotypes had to be chosen. Simon's specimens from St. Vincent Island are in the British Museum (Natural History).

The O.P.-Cambridge collection is at Oxford University, where they were placed to permit freer access than would have been possible at the British Museum.[1] Unfortunately, though the Hope Department of Entomology has both the Blackwall and the Cambridge collections, they never have succeeded in getting sufficient curatorial help. The faded labels of the Cambridge collection are nearly illegible, so that specimens are difficult to find. Cambridge specimens described in the Biologia Centrali-Americana volumes are stored in the British Museum (Natural History) in London.

[1] A. W. P.-Cambridge, 1918, Memoir of the Reverend Octavius Pickard-Cambridge, Oxford.

Thorell's types, as far as is known, are distributed in many museums. We were told that several small institutions in Europe own type specimens of Thorell. Thorell did not indicate where his specimens were deposited, and they are virtually impossible to find. Many collections worked over by Thorell, however, are in the care of the Museo Civico di Storia Naturale, Genova, and some specimens are in the Naturhistoriska Riksmuseum, Stockholm. It is believed that many types of Thorell (for instance those of his Labrador collection and of most of his American spiders) are no longer in existence.

L. Koch types are kept in the British Museum (Natural History) in London.

Compared to specimens deposited in American museums, the types in the European museums visited are in far better physical condition. The specimens apparently have never been exposed to tannic acid of corks, the sulphur of rubber stoppers, or to drying out. They have always been kept in small cotton-plugged vials in larger jars, as is now the practice in this country.

Methods of study. Many type species of genera are known from only one specimen, sometimes juvenile, making their study, recognition and generic placement extremely difficult or impossible, and accounting for the remaining uncertainties. For adequate generic diagnosis, a knowledge of the genitalia of mature individuals of both sexes is essential.

Genera based on nominal species whose types were lost had to be ignored if their descriptions were inadequate.

The numerous fossil genera had to be ignored. Leg length and position of eyes, the characters most commonly used by paleontologists, can not be used alone to delimit genera, certainly not to diagnose species.

Only one type, that of *Dubiaranea* Mello-Leitão in the Museum in Rio de Janeiro, was not available to us. The description indicates that it is a Linyphiidae.

Many genera described in the Theridiidae were found to belong to other families. Probably similar revisions of other families will turn up genera that have to be placed in the Theridiidae.

The genitalia were examined in the usual way: Female epigyna were drawn in ventral view. After clearing in clove oil, the cleared epigynum was figured, showing the ducts and seminal receptacles. Often, with the specimen immersed in clove oil, three sides of the epigynum were cut, and the epigynum folded to the side to illustrate the dorsal aspect. Even though essential

for a careful study, mounting the epigynum on a microscope slide is recommended only when many specimens are available. Not only is the epigynum more likely to be lost if imbedded in the relatively impermanent mounting medium, but there is also a likelihood that parts may warp if the mounting is not carefully done. (For specific diagnosis the illustration of the dorsal side of the epigynum is essential in most groups of Theridiidae, and the cleared ventral view in *Dipoena*). The palpi were drawn from the ventral side. In order to do this, some had to be amputated and later placed in a small (2x10 mm) vial plugged with cotton and kept with the specimen. The anatomy of the palpus was studied either by heating the palpus in 10 per cent sodium hydroxide for several minutes before transferring to distilled water, or by carefully teasing the palpus with fine needles. Often the latter method can be used without damage to any parts. A 10 per cent solution of sodium hydroxide may warp sclerites. Therefore, type species based on single males having just one palpus could be examined only superficially, and unique females often did not have their genitalia examined under a compound microscope.

The examination of cheliceral teeth was done under the dissecting microscope (144x magnification), and it may be possible that small denticles were overlooked. Even large teeth on colorless specimens are difficult to see. In common species the chelicerae were removed and examined under a compound or phase microscope. The examination of the colulus, while often easy, may be extremely difficult on minute colorless or white specimens in poor preservation.

In this paper, type species of valid genera and of genera considered synonyms for the first time are illustrated. An exception is that some American genera considered synonyms are illustrated in several papers in preparation. Several well known genera do not have the type species illustrated but have illustrations showing some of the diagnostic characters. The type species of these genera have been illustrated in revisions of American or European species.

An application to the International Commission on Zoological Nomenclature requests that its plenary powers be used to permit established usage of the generic names *Argyrodes, Robertus* and *Theonoe*, and to designate the type species for the genus *Dipoenura*.

Abbreviations used are: AMNH (American Museum of Natural History, New York); BMNH (British Museum, Natural History, London); HDE (Hope Department of Entomology, Oxford University, Oxford); MCZ (Museum of Comparative Zoology, Harvard University, Cambridge); MCSN (Museo Civico de Storia Naturale, Genova); MNHN (Muséum National d'Histoire Naturelle, Paris); NRS (Naturhistoriska Riksmuseum, Stockholm); PAS (Zoological Institute, Polish Academy of Sciences, Warsaw); SMF (Senckenberg Museum, Frankfurt).

Synonyms are subjective unless marked objective or OS. Valid genera recognized here are printed in capitals, synonyms in italics, and genera transferred to other families are in brackets.

Family THERIDIIDAE Sundevall

Theridiides Sundevall, 1833, Conspectus Arachnidum, p. 15 (an invalid original spelling for Theridiidae). Corrected to Theridiidae by later authors and listed in Official Index of Names for Taxa Belonging to the Family-Group Category in 1958 (Opinions and Declarations by the Int. Comm. Zool. Nomencl. no. 517). The invalid original spelling Theridiides and the erroneous subsequent spelling Theridionidae Simon, 1881, are listed in the Official Index of Rejected and Invalid Family-Group Names in Zoology. Type genus: *Theridion*.

NOMINAL GENERA IN ALPHABETICAL ORDER

Acanthomysmena Mello-Leitão, 1944, Rev. Museo La Plata, n.s., Zoologia, vol. 3, p. 323. Type species by original designation and monotypy: *A. spinifera* Mello-Leitão, 1944, *ibid.*, p. 324, fig. 4, ♂, from Argentina (Museum at La Plata, examined). Synonym of *Euryopis*.

Achaea O.P.-Cambridge, 1882, Proc. Zool. Soc. London, p. 428. Type species by monotypy: *A. insignis* O.P.-Cambridge, 1882, *ibid.*, pl. 30, fig. 5, ♂, from South America (HDE). [= *A. trapezoidalis* (Taczanowski)]. Homonym of *Achaea* Huebner, 1823. Objective synonym of *Achaearanea*.

ACHAEARANEA Strand, 1929, Acta Univ. Latviensis, vol. 20, pl. 11. New name for *Achaea* O.P.-Cambridge preoccupied. Synonyms: *Achaea* (OS), *Cryptachaea*, *Parasteatoda*, *Hentziectypus*.

Allodipoena Bryant, 1947, Psyche, vol. 54, p. 184. Type species by original designation and monotypy: *A. dianae* Bryant, 1947, *ibid.*, p. 184, figs. 1-4, ♀ ♂, from Puerto Rico (MCZ, examined) [= *Theridion atropunctatum* Petrunkevitch]. Synonym of *Theridion*.

Allotheridion Archer, "1946" [1947], Paper Alabama Mus. Nat. Hist., no. 22, p. 41. Type species by original designation: *Theridium murarium* Emerton, 1882, Trans. Connecticut Acad. Sci., vol. 6, p. 11, pl. 1, fig. 5, ♀ ♂, from the United States (MCZ, examined). Synonym of *Theridion*.

[*Anania* Thorell, 1895, Descriptive Catalogue of the Spiders of Burma, p. 148. Type species by monotypy: *A. bituberculata* Thorell, 1895, *ibid.*, from Burma (MCSN, examined). Homonym of *Anania* Huebner, 1823. Synonym of *Artonis*, Argiopidae.]

Ancocoelus Simon, 1894, Histoire Naturelle des Araignées, vol. 1, p. 581. Type species by original designation and monotypy: *A. livens* Simon, 1895, Ann. Soc. Ent. France, vol. 64, p. 150, ♀, from Tasmania (MNHN, examined). Synonym of *Steatoda*.

Ancylorrhanis Simon, 1894, Histoire Naturelle das Araignées, vol. 1, p. 592. Type species by original designation and monotypy: *Pholcomma hirsuta* Emerton, 1882, Trans. Connecticut Acad. Sci., vol. 6, p. 29, pl. 6, fig. 6, ♀ ♂, from North America (MCZ, examined). Synonym of *Pholcomma*.

Anelosimus Simon, 1891, Ann. Soc. Ent. France, vol. 60, p. 11. Type species by monotypy: *A. socialis* Simon, 1891, *ibid.*, from Venezuela (MNHN) [= *A. eximius* (Keyserling)]. Synonym: *Kochiura*.

Archerius Levi, 1957, Trans. Amer. Micros. Soc., vol. 76, p. 114. Type species by original designation and monotypy: *A. mendocino* Levi, 1957, *op. cit.*, p. 115, figs. 38-47, ♀ ♂, from California (AMNH, examined). Synonym of *Comaroma*.

Arctachaea Levi, 1957, Psyche, vol. 64, p. 102. Type species by original designation: *A. pelyx* Levi, 1957, *op. cit.*, p. 104, pl. 8, figs. 3-6, 12, 13, map 1, ♀ ♂, from western North America (AMNH, examined). Synonym of *Chrysso*.

Argyria Yaginuma, 1957, Acta Arachnologica, vol. 15, p. 11. Type species by original designation and monotypy: *A. venusta* Yaginuma, 1957, *ibid.*, fig. 1, ♀ ♂, from Japan (examined). Homonym of *Argyria* Huebner, 1818 and *Argyria* Robineau-Desvoidy, 1863. Synonym of *Chrysso*.

Argyroaster Yaginuma, 1958, Acta Arachnologica, vol. 15, p. 37. New name for *Argyria* Yaginuma, 1957, preoccupied. (Not *Argyraster* Nakatsudi, 1948, an opilionid.) Synonym of *Chrysso*.

Argyrodes Simon, 1864, Histoire Naturelle des Araignées, 1st ed., p. 253. Type species by tautonymy: *Linyphia argyrodes* Walckenaer, 1837, Histoire Naturelle des Insectes Aptères, vol. 2, p. 282 Thorell (1869, Nova Acta Reg. Soc. Sci. Uppsala, ser. 3, vol. 7, p. 80) has designated *A. cpeirae* Simon the type, a nominal species not originally included and thus not available. Homonym of *Argyrodes* Guenée, 1845. Synonyms: *Ariadne, Ariamnes, Rhomphaea, Conopistha, Faiditus, Bellinda, Argyrodina* (OS), *Neospintharus*. Usage strongly favors *Argyrodes* Simon since the senior homonym has not been used. (*Ariamnes* and *Rhomphaea* are older but have been used less than *Conopistha;* the latter has been in use for the last twenty years.)

Argyrodina Strand, 1928, Arch. Naturgesch., vol. 92, p. 42. New name for *Argyrodes* Simon, 1864, preoccupied. Objective synonym of *Argyrodes*.

Argyroelos Hogg, 1922, Proc. Zool. Soc. London, p. 288. Type species by monotypy: *A. micans* Hogg, 1922, *ibid.*, fig. 2, ♀, from Annam (BMNH, examined). Synonym of *Steatoda*.

Ariadne Doleschall, 1857, Nat. Tijdschr. Nederland Indie, vol. 13, p. 410. Type species by monotypy: *A. flagellum* Doleschall, 1857, *op. cit.*, p. 411, table 1, fig. 1, ♀, from Amboina Isl., South China Seas (in the Rijksmuseum, Leiden, examined). Homonym of *Ariadne* Horsfield, 1826; *Ariadne* Agassiz, 1845. Synonym of *Argyrodes*.

Ariamnes Thorell, 1869, Nova Acta Reg. Soc. Sci. Uppsala, ser. 3, vol. 7, p. 37. New name for *Ariadne* Doleschall, 1857, preoccupied. Synonym of *Argyrodes*.

Armigera Marples, 1956, Rec. Auckland Inst. Mus., vol. 4, p. 335. Type species by monotypy: *A. turbotti* Marples, 1956, *op. cit.*, p. 336, fig. 4, ♂, from New Zealand (in the Auckland Museum). Synonym of *Pholcomma*.

[*Artonis* Simon, 1895, Histoire Naturelle des Araignées, vol. 1, p. 922. New name for *Anania* Thorell, preoccupied. Transferred to Argiopidae.]

Asagena Sundevall, 1833, Conspectus Arachnidum, p. 19. Type species designated by Thorell, 1869, Nova Acta Reg. Soc. Sci. Uppsala, ser. 3, vol. 7, p. 97. *Asagena phalerata* (Panzer, 1801), Fauna Ins. Germ., no. 21, from Europe. Synonym of *Steatoda*.

Asagenella Schenkel, 1937, Festschr. Strand, vol. 3, p. 380. Type species by original designation: *Theridion erigoniformis* O.P.-Cambridge, 1872, Proc. Zool. Soc. London, p. 284, ♀ ♂, from Jordan (HDE, examined). Synonym of *Steatoda*.

Ataulfo O.P.-Cambridge, 1896, Biologia Centrali-Americana, Araneidea, vol. 1, p. 178. Type species by monotypy: *A. nugax* O.P.-Cambridge, 1896, *ibid.*, pl. 22, fig. 7, ♂, from Mexico (BMNH) [= *Stemmops bicolor* O.P.-Cambridge]. Objective synonym of *Stemmops*.

Atkinia Strand, 1929, Acta Univ. Latviensis, vol. 20, p. 14. New name for *Atkinsonia* O.P.-Cambridge, preoccupied. Synonym of *Euryopis*.

Atkinsonia O.P.-Cambridge, "1879" [1880], Proc. Zool. Soc. London, p. 691. Type species by monotypy: *A. nana* O.P.-Cambridge, 1879, *ibid.*, pl. 53, fig. 10, ♀ ♂, from New Zealand (HDE examined). Homonym of *Atkinsonia* Stainton, 1859. Synonym of *Euryopis*.

Audifia Keyserling, 1884, Die Spinnen Amerikas, Theridiidae, pt. 1, p. 209. Type species by monotypy: *A. laevithorax* Keyserling, 1884, *op. cit.*, p. 210, ♀, from Brazil (MNHN, examined).

Bellinda Keyserling, 1884, Die Spinnen Amerikas, Theridiidae, pt. 1, p. 216. Type species by monotypy: *Theridion cancellatum* Hentz, 1850, Jour. Boston Soc. Nat. Hist., vol. 6, p. 278. Synonym of *Argyrodes*.

Brontosauriella Bristowe, 1938, Ann. Mag. Nat. Hist., ser. 11, vol. 2, p. 71. Type species by monotypy: *B. melloleitaoni* Bristowe, 1938, *op. cit.*, p. 72, figs. 8-13, ♂, from Brazil (BMNH, examined). Synonym of *Thymoites*.

[*Calodipoena* Gertsch and Davis, 1936, Amer. Mus. Novitates, no. 881, p. 8. Type species by original designation and monotypy: *C. incredula* Gertsch and Davis, 1936, *ibid.*, figs. 32, 33, ♀ ♂, from Texas (AMNH, examined). Synonym of *Mysmena;* transferred to Symphytognathidae.]

[*Centropelma* L. Koch, 1872, Die Arachniden Australiens, p. 246. Type species by monotypy: *C. bicolor* L. Koch, 1872, *ibid.*, pl. 20, figs. 5, 6, ♀ ♂, from Australia. Homonym of *Centropelma* Sclater and Salvin, 1869. Synonym of *Nicodamus*.]

Cephalobares O.P.-Cambridge, "1870" [1871], Proc. Zool. Soc. London, p. 734. Type species by monotypy: *C. globiceps* O.P.-Cambridge, 1870, *op. cit.*, p. 735, pl. 44, fig. 4, ♂, from Ceylon (HDE, examined).

[*Cepheia* Simon, 1894, Histoire Naturelle des Araignées, vol. 1, p. 589. Type species by original designation and monotypy: *Theonoe longiseta* Simon, 1881, Les Arachnides de France, vol. 5, p. 132, ♀ ♂, from southern France (MNHN, examined). Transferred to Symphytognathidae.]

Cerocida Simon, 1894, Histoire Naturelle des Araignées, vol. 1, p. 508. Type species by original designation and monotypy: *C. strigosa* Simon, 1894, *ibid.*, ♀, from Venezuela (MNHN, examined).

Chacoca Badcock, 1932, Jour. Linn. Soc. London, Zool., vol. 38, p. 9. Type species designated by Bonnet, 1956: *C. antherata* Badcock, 1932, *op. cit.*, p. 10, fig. 5, ♂, from Paraguay (BMNH, examined) [= *Latrodectus curcaviensis* (Müller)]. Synonym of *Latrodectus*.

Chindellum Archer, 1950, Paper Alabama Mus. Nat. Hist., vol. 30, p. 12. Type species by original designation: *Theridion intervallatum* Emerton, 1915, Trans. Connecticut Acad. Sci., vol. 20, p. 136, pl. 1, fig. 1, ♂, from New Hampshire (MCZ, examined) [= *Theridion crispulum* Simon]. Synonym of *Theridion*.

[*Chorizoopes* O.P.-Cambridge, 1870, Proc. Zool. Soc. London, p. 737. (= *Chorizopes*, Thorell, 1895.) Type species by monotypy: *C. frontalis* O.P.-Cambridge, 1870, *op. cit.*, p. 738, pl. 44, fig. 6, ♀, from Ceylon (MNHN, examined). Transferred to Argiopidae.]

Chrosiothes Simon, 1894, Histoire Naturelle des Araignées, vol. 1, p. 521. Type species by original designation and monotypy: *C. silvaticus* Simon, 1894, *ibid.*, ♀, from Venezuela (MNHN, examined). Synonym: *Theridiotis*.

Chrysso O.P.-Cambridge, 1882, Proc. Zool. Soc. London, p. 429. Type species by original designation: *C. albomaculata* O.P.-Cambridge, 1882, *ibid.*, pl. 30, fig. 6, ♂ ♀, from the Amazon (HDE, examined) [= *C. elegans* (Taczanowski)]. Synonyms: *Meotipa*, *Physcoa*, *Argyria*, *Argyroaster*, *Arctachaea*.

Coleosoma O.P.-Cambridge, 1882, Proc. Zool. Soc. London, p. 426. Type species by monotypy: *C. blandum* O.P.-Cambridge, 1882, *op. cit.*, p. 427, pl. 29, fig. 3, ♂, from Ceylon (HDE, examined).

Comaroma Bertkau, 1889, Verhandl. Naturhist. Ver. Preuss. Rheinland Westfalen, vol. 46, p. 74. Type species by monotypy: *C. simoni* Bertkau, 1889, *ibid.*, p. 74 from southeastern Europe. (SMF, specimens determined by Wiehle examined; types examined by O. Kraus.) Synonym: *Archerius*.

Conopistha Karsch, 1881, Berliner Ent. Zeitschr., vol. 25, p. 39. Type species by original designation and monotypy: *C. Bona Dea* Karsch, 1881, *ibid.*, ♀ ♂, from Japan (probably lost). Synonym of *Argyrodes.*

Coressa Simon, 1894, Histoire Naturelle des Araignées, vol. 1, p. 647. Type species by original designation and monotypy: *Walckenaera minutissima* O.P.-Cambridge, 1879, Ann. Mag. Nat. Hist., ser. 5, vol. 4, p. 203, pl. 12, fig. 7, from Europe. Synonym of *Theonoe.*

Coscinida Simon, 1894 (October), Histoire Naturelle des Araignées, vol. 1, p. 529. Type species by original designation: *C. tibialis* Simon, 1895, Ann. Soc. Ent. France, vol. 64, p. 137, ♀ ♂, from Algeria (MNHN, examined). Synonyms: *Loxonychia, Theridiella.*

Craspedisia Simon, 1894, Histoire Naturelle des Araignées, vol. 1, p. 580. Type species by original designation and monotypy: *Umfila cornuta* Keyserling, 1891, Die Spinnen Amerikas, Brasilianische Spinnen, p. 222, pl. 8, fig. 163, ♂, from Brazil (BMNH, examined).

Crustulina Menge, 1868, Schrift. Naturf. Gesell. Danzig, n.s., vol. 2, p. 168. Type species by monotypy: *Theridium guttatum* Wider, 1834, *in* Reuss, Abhandl. Mus. Senckenbergianum, vol. 1, p. 241, tab. 16, fig. 7, ♀ ♂, from Europe.

Cryptachaea Archer, "1946" [1947], Paper Alabama Mus. Nat. Hist., no. 22, p. 36. Type species by original designation: *Theridion catapetraeum* Gertsch and Archer, 1942, Amer. Mus. Novitates, no. 1171, p. 10, fig. 7, ♀, from Florida (AMNH, examined) [= *Achaearanea porteri* (Banks)]. Synonym of *Achaearanea.*

Ctenium Menge, 1871, Schrift. Naturf. Gesell. Danzig, n.s., vol. 2, p. 292. Type species by monotypy: *Erigone pinguis* Westring, 1861, Araneae Suecicae, p. 269, ♀ ♂, from Europe [= *Robertus lividus* (Blackwall)]. Synonym of *Robertus.*

Cyllognatha L. Koch, 1872, Die Arachniden Australiens, p. 248. Type species by monotypy: *C. subtilis* Koch, 1872, *op. cit.*, p. 249, pl. 20, fig. 7, ♀ ♂, from Samoa (BMNH, examined).

Deliana Keyserling, 1886, Die Spinnen Amerikas, Theridiidae, pt. 2, p. 35. Type species by monotypy: *D. spinithorax* Keyserling, 1886, *ibid.*, ♀, from Brazil (PAS, examined). Synonym of *Dipoena.*

Diaprocorus Simon, 1894, Histoire Naturelle des Araignées, vol. 1, p. 529. Type species by original designation and monotypy: *D. multipunctatus* Simon, 1895, Ann. Soc. Ent. France, vol. 64, p. 137, ♀, from Australia (MNHN, examined). Synonym of *Euryopis.*

Dipoena Thorell, 1869, Nova Acta Reg. Soc. Sci. Uppsala, ser. 3, vol. 7, p. 91. Type species by original designation: *Atea melanogaster* C. L. Koch, 1837, Uebersicht Arachn. Syst., vol. 1, p. 4, from Germany. Synonyms: *Pachydactylus, Lasaeola, Deliana, Umfila, Trigonobothrys, Stictoxena* and *Paoningia.*

Dipoenoides Chamberlin, 1925, Bull. Mus. Comp. Zool., vol. 67, no. 4, p. 215. Type species by original designation and monotypy: *D. apachecus* Chamberlin, 1925, *ibid.*, ♂, from Arizona (MCZ, examined) [= *Euryopis scriptipes* Banks]. Synonym of *Euryopis.*

Dipoenura Simon, 1908, Bull. Sci. France, Belgique, vol. 42, p. 95. Type species *D. fimbriata* Simon, 1908, *ibid.*, ♀ ♂, from Tonkin, Indochina (MNHN, examined). Bonnet, 1956, Bibliographia Araneorum, vol. 2, p. 1515 discussed the type designation problem of this genus. In the interests of nomenclatural stability we have followed Bonnet.

Drepanodus Menge, 1869, Schrift. Naturf. Gesell. Danzig, n.s., vol. 2, p. 241. Type species by monotypy: *D. obscurus* Menge, 1869, *op. cit.*, p. 242, pl. 47, tab. 141, from Europe [= *Enoplognatha thoracica* (Hahn)]. Homonym of *Drepanodus* Pander, 1856. Synonym of *Enoplognatha*.

[*Dubiaranea* Mello-Leitão, 1943, Arq. Mus. Nac. Rio de Janeiro, vol. 37, p. 166. Type species by original designation and monotypy: *D. argenteovittata* Mello-Leitão, 1943, *op. cit.*, p. 167, fig. 10, ♀, from Rio Grande do Sul (in the Museo Nacional, Rio de Janeiro, not available for study). Probably Linyphiidae.]

[*Eidmannella* Roewer, 1935, Veröff. Deutschen Kolonial Uebersee Mus., ser. 1, vol. 2, p. 195. Type species by monotypy: *E. attae* Roewer, 1935, *op. cit.*, p. 196, tab. 10, fig. 3, ♀ ♂, from Brazil (SMF, examined) [= *Nesticus pallidus* Emerton]. In family Nesticidae.]

Emertonella Bryant, 1945, Psyche, vol. 52, p. 182. Type species by original designation and monotypy: *Euryopis emertoni* Bryant, 1933, Bull. Mus. Comp. Zool., vol. 74, no. 6, p. 172, pl. 1, fig. 1, ♂, from southeastern United States (MCZ, examined). Synonym of *Euryopis*.

Enoplognatha Pavesi, 1880, Ann. Mus. Civ. Stor. Nat. Genova, vol. 15, p. 325. Type species by original designation and monotypy: *Theridion mandibulare* Lucas, "1849" [1846], Expl. Sci. Algérie Zool., vol. 1, p. 260, pl. 17, fig. 1, ♂, from Europe. *Enoplognatha* is listed in the Official List of Generic Names in Zoology, name no. 1273, Opinion 517, 1958. Synonyms: *Drepanodus, Phyllonethis, Symopagia, Marmatha*, and *Rugatha*.

[*Enthorodera* Simon, 1907, Ann. Mus. Civ. Stor. Nat. Genova, vol. 43, p. 264. Type species by monotypy: *E. atricolor* Simon, 1907, *op. cit.*, p. 265, ♀, from Africa (MCSN, examined). Transferred to Theridiosomatidae.]

[*Epecthina* Simon, 1895, Histoire Naturelle des Araignées, vol. 1, p. 924. Type species by original designation and monotypy: *E. circinata* Simon. Family Symphytognathidae.]

[*Epecthinula* Simon, 1903, Ann. Soc. Ent. Belgique, vol. 47, p. 27. Type species by monotypy: *E. minutissima* Simon, 1903, *ibid.*, p. 27, from Jamaica. Family Symphytognathidae.]

Episinopsis Simon, 1894, Histoire Naturelle des Araignées, vol. 1, p. 522. Type species by original designation: *E. rhomboidalis* Simon, 1895, Ann. Soc. Ent. France, vol. 64, p. 163, ♀, from Malaya (MNHN, examined). Synonym of *Episinus*.

Episinus Latreille, 1809, Genera Crustaceorum et Insectorum, vol. 4, p. 371. Type species by monotypy: *E. truncatus* Latreille, 1809, *ibid.*, from Europe. Synonyms: *Moneta, Janulus, Penictis, Plocamis, Episinopsis, Hyocrea, Hyptimorpha*, and *Janula*.

Eucharia C. L. Koch, "1836" [? 1835], *in* Panzer, Faunae Insectorum Germaniae, Heft 134 [not seen]. According to Bonnet, 1956, Bibliographia Araneorum, vol. 2, p. 1805, *E. bipunctata* and *E. hera* (= *castanea*) are types. Preoccupied by *Eucharia* Hübner, 1802. Synonym of *Steatoda*.

Euryopis Menge, 1868, Schrift. Naturf. Gesell. Danzig, n.s., vol. 2, p. 174. Type species designated by Thorell, 1869, Nova Acta Reg. Soc. Sci. Uppsala, ser. 3, vol. 7, p. 96: *E. flavomaculata* (C. L. Koch), 1836, Die Arachniden, vol. 3, p. 67, fig. 220, ♀, from Europe. Synonyms: *Phycus, Atkinsonia, Phycosoma, ?Mastostigmus, Phylarchus, Diaprocorus, Dipoenoides, Atkinia, Acanthomysmena, Emertonella,* and *Mufila*.

[*Euxinella* Drensky, 1938, Festschr. Strand, vol. 4, p. 570. Type species by monotypy: *E. strandi* Drensky, 1938, *op. cit.*, p. 571, ♀ ♂, from Bulgaria (Naturhistorisches Museum, Sofia, examined). [Close to *Titanoeca albomaculata* (Lucas).] Transferred to Amaurobiidae.]

Faiditus Keyserling, 1884, Die Spinnen Amerikas, Theridiidae, pt. 1, p. 158. Type species designated by Petrunkevitch, 1928, Trans. Connecticut Acad. Sci., vol. 29, p. 118: *F. ecaudatus* Keyserling, 1884, *ibid.*, p. 158, pl. 7, fig. 9, from northeastern South America, ♀, (PAS, examined). Synonym of *Argyrodes*.

Formicinoides Keyserling, 1884, Die Spinnen Amerikas, Theridiidae, pt. 1, p. 213. Type species designated by Simon, 1894, Histoire Naturelle des Araignées, vol. 1, p. 508: *F. brasiliana* Keyserling, 1884, *op. cit.*, p. 214, pl. 10, fig. 128, ♀, from the Amazon (MNHN, examined). Synonym of *Helvibis*.

Garricola Chamberlin, 1916, Bull. Mus. Comp. Zool., vol. 60, p. 231. Type species by original designation and monotypy: *G. sanctus* Chamberlin, 1916, *ibid.*, pl. 16, figs. 5-7, ♀, from Peru (MCZ, examined). Synonym of *Thymoites*.

Garritus Chamberlin and Ivie, 1933, Bull. Univ. Utah, biol. ser., vol. 2, no. 2, p. 9. Type species by original designation and monotypy: *G. vigerens* Chamberlin and Ivie, 1933, *ibid.*, pl. 2, figs. 10 20, ♀ ♂, from Utah (in the University of Utah Collection). Synonym of *Robertus*.

Gnophomytis Simon, 1894, Histoire Naturelle des Araignées, vol. 1, p. 560. Type species by original designation and monotypy: *G. variolosa* Simon, 1895, Ann. Soc. Ent. France, vol. 64, p. 148, ♀, from Venezuela. No specimens known to exist. Species description not recognizable. May be a synonym of *Phoroncidia*.

Helvibis Keyserling, 1884, Die Spinnen Amerikas, Theridiidae, pt. 1, p. 172. Type species designated by Simon, 1894, Histoire Naturelle des Araignées, vol. 1, p. 507: *H. thorelli* Keyserling, 1884, *ibid.*, ♀, from Peru (BMNH, examined). Synonym: *Formicinoides*.

Hentziectypus Archer, "1946" [1947], Paper Alabama Mus. Nat. Hist., no. 22, p. 51. Type species by original designation: *Theridion globosum* Hentz, 1850, Jour. Boston Soc. Nat. Hist., vol. 6, p. 279, pl. 9, fig. 23, from Alabama. Synonym of *Achaearanea*.

Heribertus Keyserling, 1886, Die Spinnen Amerikas, Theridiidae, pt. 2, p. 27. Type species by monotypy: *H. rubromaculatus* Keyserling, 1886, *op. cit.*, p. 28, ♂, from Brazil (MNHN, examined). Synonym of *Phoroncidia.*

Hetschkia Keyserling, 1886, Die Spinnen Amerikas, Theridiidae, pt. 2, p. 246. Type species by monotypy: *H. gracilis* Keyserling, 1886, *op. cit.*, p. 247, ♂, from Brazil (BMNH, examined).

[*Hexablemma* Berland, 1920, Aranea II *in* Voy. Alluaud et Jeannel Afrique Orientale, p. 167. Type species by monotypy: *H. cataphractum* Berland, 1920, *ibid.*, figs. 205-210, ♀, from Africa (MNHN, examined). Belongs to Tetrablemmidae.]

Hildbolda Keyserling, 1884, Die Spinnen Amerikas, Theridiidae, pt. 1, p. 157. Type species by monotypy: *H. simoni* Keyserling, 1884, *ibid.*, pl. 7, fig. 97, specimens labeled from Brazil [misprinted as Massachusetts] (MNHN, examined). Synonym of *Thwaitesia.*

Histagonia Simon, 1894, Histoire Naturelle des Araignées, vol. 1, p. 585. Type species by original designation and monotypy: *H. deserticola* Simon, 1894, *ibid.*, ♀ ♂, from South Africa (MNHN, examined).

Hubba, O.P.-Cambridge, 1897, Biologia Centrali-Americana, Araneidea, vol. 1, p. 231. Type species by monotypy: *H. insignis* O.P.-Cambridge, 1897, *ibid.*, pl. 30, fig. 4, ♂, from Guatemala (BMNH). Synonym of *Thymoites.*

Hyocrea Simon, 1894, Histoire Naturelle des Araignées, vol. 1, p. 559. Type species by original designation and monotypy: *H. implexa* Simon, 1895, Ann. Soc. Ent. France, vol. 64, p. 147, ♀, from Venezuela (MNHN, examined). Synonym of *Episinus.*

Hypobares Simon, 1894, Histoire Naturelle des Araignées, vol. 1, p. 552. Type species by original designation and monotypy: *H. unisignatus* Simon, 1895, Ann. Soc. Ent. France, vol. 64, p. 144, ♂, from Venezuela (MNHN, examined). Synonym of *Thymoites.*

Hyptimorpha Strand, 1906, Abh. Senckenberg Ges., vol. 30, p. 135. Type species by original designation and monotypy: *H. mirabilis* Bösenberg and Strand, 1906, *op. cit.*, p. 136, pl. 11, fig. 227, ♀, from Japan (SMF, examined). Synonym of *Episinus.*

Iardinis Simon, 1899, Ann. Soc. Ent. Belgique, vol. 43, p. 87. Type species by monotypy: *I. weyseri* Simon, 1899, *ibid.*, ♀, from Sumatra. No specimens known to exist. Species description not recognizable. Probably in Pholcidae. Might be a synonym of *Styposis.*

Icona Forster, 1955, Rec. Dominion Mus., vol. 2, p. 189. Type species by original designation and monotypy: *I. alba* Forster, 1955, *op. cit.*, p. 190, figs. 35-39, ♀ ♂, from Auckland Isl. south of New Zealand (Canterbury Museum, New Zealand, examined).

Janula Strand, 1932, Folia Zool. Hydrobiol., vol. 4, p. 139. New name for *Janulus* Thorell, preoccupied. Synonym of *Episinus.*

Janulus Thorell, 1881, Ann. Mus. Civ. Stor. Nat. Genova, vol. 17, p. 163. Type species by original designation and monotypy: *J. bicornis* Thorell, 1881, *ibid.*, ♀, from Cape York, Australia. Homonym of *Janulus* Lowe, 1852. Synonym of *Episinus.*

Kochiura Archer, 1950, Paper Alabama Mus. Nat. Hist., no. 30, p. 16. Type species by original designation and monotypy: *Theridium aulicum* C. L. Koch, 1838, Die Arachniden, vol. 4, p. 115, fig. 323, ♀, from Europe. Synonym of *Anelosimus*.

Lasaeola Simon, 1881, Les Arachnides de France, vol. 5, p. 136. New name for *Pachydactylus* Menge, 1868, preoccupied. Synonym of *Dipoena*.

Latrodectus Walckenaer, 1805, Tableau des Aranéides, p. 81. Type species designated by Latreille, 1810, Considérations général sur l'ordre natural des Animaux, p. 424; *Aranea 13-guttatus* Rossi, 1794, Fauna Etrusca Aranea, vol. 2, p. 136, pl. 9, fig. 13 [= *L. mactans tredecimguttatus* (Rossi)], from Mediterranean countries. Synonym: *Chacoca*.

[*Liger* O.P.-Cambridge, 1896, Biologia Centrali-Americana, Araneidea, vol. 1, p. 210. Type species by monotypy: *L. incompta* O.P.-Cambridge, 1896, *ibid.*, pl. 28, fig. 6, ♂, from Guatemala (BMNH, examined). Transferred to Linyphiidae.]

Lithyphantes Thorell, 1869, Nova Acta Reg. Soc. Sci. Uppsala, ser. 3, vol. 7, no. 5, p. 94. Type species by original designation and monotypy: *Aranea carollata* Linnaeus, 1758, Systema Naturae, ed. 10, vol. 1, p. 621, from Europe and North America [= *Steatoda albomaculata* (De Geer)]. Synonym of *Steatoda*.

Loxonychia Tullgren, 1910, *in* Sjoestedt, Ergeb. Schwedischen Exped. in Kilimandjaro, vol. 3, p. 125. Type species by monotypy: *L. lugubris* Tullgren, 1910, *ibid.*, pl. 2, fig. 40, ♂, from Kilimanjaro, east Africa (NRS, examined). Synonym of *Coscinida*.

Marmatha Chamberlin and Ivie, 1942, Bull. Univ. Utah, biol. ser., vol. 7, no. 1, p. 40. Type species by original designation: *Theridion marmoratum* Hentz, 1850, Jour. Boston Soc. Nat. Hist., vol. 6, p. 273, pl. 9, fig. 3, ♀, from North America. Synonym of *Enoplognatha*.

Mastostigmus Simon, "1888" [1889], Ann. Soc. Ent. France, ser. 6, vol. 8, p. 230. Type species by monotypy: *M. decemperlatus* Simon, 1888, *ibid.*, ♂, from Madagascar. No specimens known to exist. Species description not recognizable. Probably a synonym of *Euryopis*.

[*Mecynidis* Simon, 1894, Histoire Naturelle des Araignées, vol. 1. p. 507. Type species by original designation and monotypy: *M. dentipalpis* Simon, 1894, *ibid.*, ♂, from Transvaal (MNHN, examined). Probably Argiopidae or Linyphiidae.]

Meotipa Simon, 1894, Histoire Naturelle des Araignées, vol. 1, p. 519. Type species by original designation: *M. picturata* Simon, 1895, Ann. Soc. Ent. France, vol. 64, p. 133, ♀, from India (MNHN, examined). Synonym of *Chrysso*.

Mesopneustes O.P.-Cambridge, 1894, Biologia Centrali-Americana, Araneidea, vol. 1, p. 126. Type species by monotypy: *M. nigrovittata* O.P.-Cambridge, 1894, *ibid.*, pl. 17, figs. 3, 4, ♂, from Mexico (BMNH) [= *Theridula gonygaster* (Simon)]. Synonym of *Theridula*.

Mettus O.P.-Cambridge, 1899, Biologia Centrali-Americana, Araneidea, vol. 1, p. 292. Type species by monotypy: *M. reclivis* O.P.-Cambridge, 1899, *op. cit.*, p. 293, pl. 38, fig. 8, ♀, from Mexico (BMNH) [= *Stemmops bicolor* O.P.-Cambridge]. Synonym of *Stemmops*.

[*Microdipoena* Banks, 1895, Jour. New York Ent. Soc., vol. 3, p. 84. Type species by monotypy: *M. guttata* Banks, 1895, *op. cit.*, p. 85, ♂, from New York (MCZ, examined). Synonym of *Mysmena*. Transferred to Symphytognathidae.]

[*Micropholcomma* Crosby and Bishop, 1927, Jour. New York Ent. Soc., vol. 35, p. 152. Type species by original designation and monotypy: *M. caeligenus* Crosby and Bishop, 1927, *ibid.*, ♂, from Australia (in collection of Cornell University, Ithaca, New York). Transferred to Symphytognathidae.]

Moero O.P.-Cambridge, 1904, Ann. South African Mus., vol. 3, p. 156. Type species by monotypy: *M. quadrimaculata* O.P.-Cambridge, 1904, *op. cit.*, p. 157, pl. 11, fig. 4, ♀ ♂, from South Africa (specimens lost). Probably a synonym of *Steatoda*.

Molione Thorell, 1892, Boll. Soc. Ent. Italiana, vol. 24, p. 215. Type species by original designation and monotypy: *M. triacantha* Thorell, 1892, *op. cit.*, p. 216, ♀, from Singapore (NRS, examined).

Moneta O.P.-Cambridge, "1870" [1871], Proc. Zool. Soc. London, p. 736. Type species by monotypy: *M. spinigera* O.P.-Cambridge, 1870, *ibid.*, pl. 44, fig. 5, ♀, from Ceylon (BMNH, examined). Synonym of *Episinus*.

Mufila Bryant, 1949, Psyche, vol. 56, p. 66. Type species by original designation and monotypy: *M. texana* Bryant, 1949, *op. cit.*, p. 67, fig. 1, ♂, from Texas (MCZ, examined) [= *Euryopis bryantae* Levi]. Synonym of *Euryopis*.

[*Mysmena* Simon, 1894, Histoire Naturelle des Araignées, vol. 1, p. 588. Type species by original designation and monotypy: *Theridion leucoplagiatum* Simon, 1879, Bull. Soc. Zool. France, vol. 4, p. 258, ♀ ♂, from southern France (MNHN, examined). Transferred to Symphytognathidae.]

[*Mysmenopsis* Simon, "1897" [1898], Proc. Zool. Soc. London, p. 865. Type species designated by Simon, 1903, Histoire Naturelle des Araignées, vol. 2, p. 991: *M. femoralis* Simon, 1897, *ibid.*, ♀, from St. Vincent Island, Lesser Antilles (BMNH, examined). Transferred to Symphytognathidae.]

Neospintharus Exline, 1950, Studies Honoring Trevor Kincaid, Univ. Washington Press, p. 112. Type species by original designation and monotypy: *N. parvus* Exline, 1950, *ibid.*, pl. 1, figs. 2, 4, ♀, from Ecuador (specimen lost). Synonym of *Argyrodes*.

Neottiura Menge, 1868, Schrift. naturf. Gesell. Danzig, n.s., vol. 2, p. 162. Type species by monotypy: *Aranea bimaculata* Linnaeus, 1767, Systema Naturae, ed. 12, p. 1033, from Europe. Synonym of *Theridion*.

Nesticodes Archer, 1950, Paper Alabama Mus. Nat. Hist., no. 30, p. 22. Type species by original designation and monotypy: *Theridion rufipes* Lucas, "1846" [1849], Expl. Sci. Algérie Zool., pt. 1, p. 263, pl. 16, fig. 5, ♀. Synonym of *Theridion*.

[*Nicodamus* Simon, "1887" [1888], Ann. Soc. Ent. France, ser. 6, vol. 7, Bull., p. cxciv. New name for *Centropelma* L. Koch preoccupied. R. R. Forster (*in lett.*) suggested that this genus belongs to the family Zodariidae.]

Onesinda O.P.-Cambridge, 1895, Proc. Dorset Nat. Club, vol. 16, p. 104. Type species by monotypy: *Walckenaera minutissima* O.P.-Cambridge, 1879, Ann. Mag. Nat. Hist., ser. 5, vol. 4, p. 203, pl. 12, fig. 7. Synonym of *Theonoe*.

Oronota Simon, 1871, Ann. Soc. Ent. France, ser. 5, vol. 1, Bull., p. vii. Type species by original designation and monotypy: *Epeira paradoxa* Lucas, "1849" [1846], Expl. Sci. Algérie Zool., vol. 1, p. 251, pl. 15, fig. 7, ♀, from Mediterranean countries. Synonym of *Phoroncidia*.

Oroodes Simon, 1873, Mem. Soc. Roy. Sci. Liége, ser. 2, vol. 5, p. 127. Type species by monotypy: *Epeira paradoxa* Lucas, "1849" [1846], Expl. Sci. Algérie Zool., vol. 1, p. 251, pl. 15, fig. 7, ♀, from Mediterranean countries. Synonym of *Phoroncidia*.

Pachydactylus Menge, 1868, Schrift. naturf. Gesell, Danzig, n.s., vol. 2, p. 176. Type species by monotypy: *P. pronus* Menge, 1868, *op. cit.*, p. 177, pl. 33, tab. 80, from Europe. Homonym of *Pachydactylus* Wiegmann, 1834. Synonym of *Dipoena*.

[*Paculla* Simon "1887" [1888], Ann. Soc. Ent. France, ser. 6, vol. 7, Bull., p. cxciv. New name for *Phaedima* Thorell, preoccupied. Belongs to family Tetrablemmidae.]

Paidisca Bishop and Crosby, 1926, Jour. Elisha Mitchell Sci. Soc., vol. 41, p. 178. Type species by original designation and monotypy: *Histagonia marxi* Crosby, 1906, Canadian Ent., vol. 38, p. 309, figs. 35-36, ♀ ♂, from North America. Synonym of *Thymoites*.

Paidiscura Archer, 1950, Paper Alabama Mus. Nat. Hist., no. 30, p. 26. Type species by original designation and monotypy: *Theridion pallens* Blackwall, 1834, Researches in Zoology, p. 357, ♀, from Europe. Synonym of *Theridion*.

Paoningia Schenkel, 1936, Arkiv Zool., vol. 29, p. 41. Type species by monotypy: *P. turriceps* Schenkel, 1936, *op. cit.*, p. 42, fig. 12, ♂, from China (NRS, examined). Synonym of *Dipoena*.

Parasteatoda Archer, "1946" [1947], Paper Alabama Mus. Nat. Hist., no. 22, p. 38. Type species by original designation: *Theridium tepidariorum* C. L. Koch, 1841, Die Arachniden, vol. 8, p. 75, figs. 646-648, ♀ ♂, from Europe. Synonym of *Achaearanea*.

PARATHERIDULA Levi, 1957, Trans. Amer. Micros. Soc., vol. 76, p. 105. Type species by original designation and monotypy: *Mysmena quadrimaculata* Banks, 1896, Trans. Amer. Ent. Soc., vol. 23, p. 66, ♀ ♂, from North America (MCZ, examined) [= *Paratheridula perniciosa* (Keyserling)].

[*Paurotylus* Tullgren, 1910, *in* Sjoestedt, Ergeb. Schwedischen Exped. Kilimandjaro, vol. 3, p. 171. Type species by monotypy: *P. depressus* Tullgren, 1910, *ibid.*, pl. 4, fig. 125, ♂, from east Africa (NRS, examined). Transferred to Argiopidae.]

Pedanostethus Simon, 1884, Les Arachnides de France, vol. 5, p. 195. New name for *Ctenium* Menge, erroneously thought preoccupied. Synonym of *Robertus*.

Penictis Simon, 1894, Histoire Naturelle des Araignées, vol. 1, p. 520. Type species by original designaton: *P. mucronata* Simon, 1894, *ibid.*, ♀, from Singapore (MNHN, examined). Synonym of *Episinus*.

[*Perania* Thorell, 1890, Ann. Mus. Civ. Stor. Nat. Genova, ser. 2, vol. 8, p. 315. Type species by original designation and monotypy: *P. pallida* Thorell, 1890, *ibid.*, from Sumatra (MCSN, examined). Probably Tetrablemmidae.]

[*Phaedima* Thorell, 1881, Ann. Mus. Civ. Stor. Nat. Genova, vol. 17, p. 232. Type species by original designation and monotypy: *P. granulosa* Thorell, 1881, *op. cit.*, p. 233, ♂ (MCSN, examined). Homonym of *Phaedima* Robineau-Desvoidy, 1863. Synonym of *Paculla*, transferred to Tetrablemmidae.]

Phaetoticus Simon, 1894, Histoire Naturelle des Araignées, vol. 1, p. 552. Type species by original designation and monotypy: *P. modestus* Simon, 1894, *ibid.*, ♀, from Ceylon (MNHN, examined). Synonym of *Theridion*.

Philto Simon, 1894, Histoire Naturelle des Araignées, vol. 1, p. 552. Type species by original designation and monotypy: *P. subtilis* Simon, 1895, Ann. Soc. Ent. France, vol. 64, p. 145, ♂, from Zanzibar (MNHN, examined). Synonym of *Thymoites*.

Pholcomma Thorell, 1869, Nova Acta Reg. Soc. Sci. Uppsala, ser. 3, vol. 7, no. 5, p. 98. Type species by original designation and monotypy: *Theridion projectum* O.P.-Cambridge, 1862, Zoologist, vol. 20, p. 7962, ♀ ♂, from Europe [= *Pholcomma gibbum* (Westring)]. Synonyms: *Ancylorrhanis, Armigera*.

Phoroncidia Westwood, 1835, Zool. Jour., vol. 5, p. 452. Type species by monotypy: *P. aculeata* Westwood, 1835, *op. cit.*, p. 453, tab. 22, fig. 9, ♀ ♂, from Malaya (MNHN, specimen determined by Berland examined). Synonyms: *Tricantha, Trithena, Oronota, Ulesanis, Stegosoma, Oroodes, Sclerogaster, Sudabe,* ? *Wibrada, Heribertus,* and *Gnophomytis*.

Phycosoma O.P.-Cambridge, "1879" [1880], Proc. Zool. Soc. London, p. 692. Type species by monotypy: *P. oecobioides* O.P.-Cambridge, 1879, *ibid.*, pl. 52, fig. 6, ♀, from New Zealand (HDE, examined). Synonym of *Euryopis*.

Phycus O.P.-Cambridge, "1870" [1871], Proc. Zool. Soc. London, p. 742. Type species by monotypy: *P. brevis* O.P.-Cambridge, 1870, *op. cit.*, p. 743, pl. 44, fig. 9, juv., from Ceylon (HDE, examined) [? = *Euryopis taczanowskii* Keyserling]. Homonym of *Phycus* Walker, 1850. Synonym of *Euryopis*.

Phylarchus Simon, "1888" [1889], Ann. Soc. Ent. France, ser. 6, vol. 8, p. 242. New name for *Phycus* O.P.-Cambridge, 1871, preoccupied. Synonym of *Euryopis*.

Phylloneta Archer, 1950, Paper Alabama Mus. Nat. Hist., no. 30, p. 19. Type species by original designation: *Theridion pictipes* Keyserling, 1884, Die Spinnen Amerikas, Theridiidae, pt. 1, p. 64, pl. 3, fig. 38, from Florida. Synonym of *Theridion*.

Phyllonethis Thorell, 1869, Nova Acta Reg. Soc. Sci. Uppsala, ser. 3, vol. 7, p. 90. Type species by original designation: *Araneus lineatus* Clerck, 1757, Svenska Spindler, p. 60, pl. 3, fig. 10, ♀, from Europe [= *Enoplognatha ovata* (Clerck)]. *Phyllonethis* has been suppressed under the Plenary Powers of the Int. Comm. Zool. Nomenel. and the name listed on the Official Index of Rejected and Invalid Generic Names in Zoology, name no. 1158, Opinion 517, 1958. Synonym of *Enoplognatha*.

Physcoa Thorell, 1895, Descriptive Catalogue of the Spiders of Burma, p. 82. Type species by original designation and monotypy: *P. scintillans* Thorell, 1895, *op. cit.*, p. 83, ♀, from Burma (BMNH, examined). Synonym of *Chrysso*.

Plocamis Simon, 1894, Histoire Naturelle des Araignées, vol. 1, p. 521. Type species by original designation and monotypy: *Episinus theridioides* Simon, 1873, Mém. Soc. Roy. Sci. Liége, ser. 2, vol. 5, p. 125, ♀, from Corsica (MNHN, examined). Synonym of *Episinus*.

Propostira Simon, 1894, Histoire Naturelle des Araignées, vol. 1, p. 510. Type species by original designation and monotypy: *P. quadrangulata* Simon, 1895, Ann. Soc. Ent. France, vol. 64, p. 132, ♀, from India (MNHN, examined). Probably a synonym of *Theridion*.

Rhomphaea L. Koch, 1872, Die Arachniden Australiens, p. 289. Type species by monotypy: *R. cometes* L. Koch, 1872, *op. cit.*, p. 290, pl. 24, fig. 3, ♀, from Samoa. Type species probably very close to *Argyrodes fictilium* (Hentz) from North America. Synonym of *Argyrodes*.

Robertus O.P.-Cambridge, 1879, Spiders of Dorset, p. 103. Type species by monotypy: *R. astutus* O.P.-Cambridge, 1879, *ibid.*, ♀, from Europe (HDE) [= *R. neglectus* O.P.-Cambridge]. Synonyms: *Ctenium, Pedanostethus, Garritus*. Usage strongly favors *Robertus* although *Ctenium* is an older available synonym.

Rugatha Chamberlin and Ivie, 1942, Bull. Univ. Utah, biol. ser., vol. 7, no. 1, p. 42. Type species by original designation: *Enoplognatha* (*Rugatha*) *pikes* Chamberlin and Ivie, *ibid.*, ♀♂, from Colorado (in the University of Utah Collection, Salt Lake City) [= *E. intrepida* Sørensen]. Synonym of *Enoplognatha*.

Rugathodes Archer, 1950, Paper Alabama Mus. Nat. Hist., no. 30, p. 24. Type species by original designation: *Theridium sexpunctatum* Emerton, 1882, Trans. Connecticut Acad. Sci., vol. 6, p. 12, pl. 2, fig. 5, ♀♂, from North America (MCZ, examined). Synonym of *Theridion*.

Sclerogaster Cavanna, 1876, Bull. Soc. Ent. Italiana, vol. 8, p. 89. Type species by monotypy: *S. pusillus* Cavanna, 1876, *ibid.*, p. 90, pl. 2, figs. 3-11, ♀♂, from Mediterranean countries [= *Phoroncidia paradoxa* (Lucas)]. Synonym of *Phoroncidia*.

[*Sedasta* Simon, 1894, Histoire Naturelle des Araignées, vol. 1, p. 531. Type species by original designation and monotypy: *S. ferox* Simon, 1894, *ibid.*, juv., from Sierra Leone (MNHN, examined). Does not belong to Theridiidae.]

Spelobion Chamberlin and Ivie, 1938, Publ. Carnegie Inst. Washington, no. 491, p. 133. Type species by original designation and monotypy: *S. spukilum* Chamberlin and Ivie, 1938, *ibid.*, ♀, from Yucatan (AMNH) [Probably = *Thymoites luculentus* (Simon)]. Synonym of *Thymoites.*

[*Spheropistha* Yaginuma, 1957, Acta Arachnologica, vol. 15, no. 1, p. 14. Type species by original designation and monotypy: *S. melanosoma* Yaginuma, 1957, *op. cit.*, p. 15, fig. 2, ♀, from Japan (examined). Transferred to Theridiosomatidae.]

Sphyrotinus Simon, 1894, Proc. Zool. Soc. London, p. 524. Type species by monotypy: *S. luculentus* Simon, 1894, *ibid.*, ♀ ♂, from St. Vincent Island, Lesser Antilles (BMNH, examined). Synonym of *Thymoites.*

Spintharus Hentz, 1850, Jour. Boston Soc. Nat. Hist., vol. 6, p. 283. Type species by monotypy: *S. flavidus* Hentz, 1850, *op. cit.*, p. 284, pl. 10, fig. 8, ♀, from Alabama.

Stearodea F.P.-Cambridge, 1902, Ann. Mag. Nat. Hist., ser. 7, vol. 9, p. 13. Type species by original designation: *Aranea bipunctata* Linnaeus, 1758, Systema Naturae, ed. 10, vol. 1, p. 620. Synonym of *Steatoda.*

Steassa Simon, 1910, Denksehr. Med. Nat. Gesell. Jena, vol. 16, p. 192. Type species by monotypy: *S. marmorata* Simon, 1910, *ibid.*, ♀, from South Africa (MNHN, examined). Synonym of *Steatoda.*

Steatoda Sundevall, 1833, Conspectus Arachnidum, p. 16. Although *Aranea bipunctata* (Linnaeus) is generally listed as the type species, the first designation seems to be by Thorell, 1869, Nova Acta Reg. Soc. Sci., Uppsala, ser. 3, vol. 7, p. 93: *S. castanea* (Clerck, 1757), Svenska Spindlar, p. 49, from Europe. Synonyms: *Asagena, Eucharia, Lithyphantes, Teutana, Stethopoma, Ancococlus, Stearodea, ?Mocro, Steassa, Argyroelus, Asagenella.*

Stegosoma O.P.-Cambridge, 1873, Proc. Zool. Soc. London, p. 126. Type species designated by Bonnet, 1958, Bibliographia Araneorum, vol. 2, p. 4149: *S. testudo* O.P.-Cambridge, 1873, *ibid.*, pl. 14, fig. 10, ♀, from Ceylon. Homonym of *Stegosoma* Loew, 1863. Synonym of *Phoroncidia.*

Stemmops O.P.-Cambridge, 1894 (January), Biologia Centrali-Americana, Araneidea, vol. 1, p. 125. Type species by monotypy: *S. bicolor* O.P.-Cambridge, 1894, *ibid.*, pl. 17, fig. 5, ♂, from Mexico (BMNH). Synonyms: *Ataulfo* (OS), *Mettus.*

Stethopoma Thorell, 1890, Ann. Mus. Civ. Stor. Nat. Genova, ser. 2, vol. 8, p. 288. Type species by original designation and monotypy: *S. cingulatum* Thorell, 1890, *op. cit.*, p. 289, ♀ ♂, from Sumatra (MCSN, examined). Synonym of *Steatoda.*

Stictoxena Simon, 1894, Histoire Naturelle des Araignées, vol. 1, p. 529. Type species by original designation and monotypy: *S. sertata* Simon, 1895, Ann. Soc. Ent. France, vol. 64, p. 138, ♂, from Ceylon (MNHN, examined). Synonym of *Dipoena.*

STYPOSIS Simon, 1894, Histoire Naturelle des Araignées, vol. 1, p. 592. Type species by original designation and monotypy: *S. flavescens* Simon, 1894, *ibid.*, ♀, from Venezuela (MNHN, examined). Synonym: ? *Iardinis*.

Sudabe Karsch, 1879, Verhandl. Naturhist. Ver. Preuss. Rhineland Westfalen, vol. 36, p. 103. Type species by original designation and monotypy: *S. pilula* Karsch, 1879, *ibid.*, ♀, from Japan. Type specimens lost. Specimens from Japan were examined. Synonym of *Phoroncidia*.

Sunitorypha Komatsu, 1960, Acta Arachnologica, vol. 17, p. 9. Type species by original designation and monotypy: *S. linyphoides* Komatsu, 1960, *ibid.*, vol. 17, p. 9, fig., ♀♂, from Japan [= *Nesticus floronoides* (Komatsu)]. Synonym of *Nesticus*, family Nesticidae.

Symopagia Simon, 1894, Histoire Naturelle des Araignées, vol. 1, p. 559. Type species by original designation and monotypy: *S. oreophila* Simon, 1895, Ann. Soc. Ent. France, vol. 64, p. 146, ♀, from Ceylon (MNHN, examined). Synonym of *Enoplognatha*.

[*Synaphris* Simon, 1894, Histoire Naturelle des Araignées, vol. 1, p. 589. Type species by original designation: *Grammonota letourneuxi* Simon, 1884, Les Arachnides de France, vol. 5, p. 599, ♂, from Egypt (MNHN, examined). Transferred to Symphytognathidae.]

SYNOTAXUS Simon, 1894, Histoire Naturelle des Araignées, vol. 1, p. 495. Type species by original designation and monotypy: *S. turbinatus* Simon, 1895, Ann. Soc. Ent. France, vol. 64, p. 131, ♂, from Brazil (MNHN, examined).

[*Tamasesia* Marples, 1955, Jour. Linn. Soc. London, Zool., vol. 42, p. 476. Type species by original designation: *T. rotunda* Marples, 1955, *ibid.*, pl. 57, figs. 14, 18, 20, 23, ♀♂, from Samoa (OM). Synonym of *Mysmena;* transferred to Symphytognathidae.]

[*Taphiassa* Simon, 1880, Ann. Soc. Ent. Belgique, vol. 23, C.R., p. clxxii. Type species by monotypy: *T. impressa* Simon, 1880, *ibid.*, ♀, from New Caledonia (MNHN, examined). Transferred to Symphytognathidae.]

[*Tekella* Urquhart, 1894, Trans. New Zealand Inst., vol. 26, p. 211. Type species by monotypy: *T. absidata* Urquhart, 1839, *ibid.*, ♂, from New Zealand (Canterbury Museum, Christchurch, examined). Transferred to Theridiosomatidae (might be Argiopidae).

TEKELLINA Levi, 1957, Trans. Amer. Micros. Soc., vol. 76, p. 107. Type species by original designation and monotypy: *T. archboldi* Levi, 1957, *ibid.*, figs. 7-12, ♀♂, from Florida (AMNH, examined).

Teutana Simon, 1881, Les Arachnides de France, vol. 5, p. 161. New name for *Eucharia* C. Koch, preoccupied. Synonym of *Steatoda*.

THEONOE Simon, 1881, Les Arachnides de France, vol. 5, p. 130. Type species designated by Simon, 1894, Histoire Naturelle des Araignées, vol. 1, p. 589: *Theonoe filiola* Simon, 1881, *op. cit.*, vol. 5, p. 131 ♀♂ [= *Theonoe minutissima* (O.P.-Cambridge)]. Homonym of *Theonoe* Philippi, 1865, a name for an hemipteran nymph. *Theonoe* Philippi has never been used. Synonyms: *Coressa*, *Onesinda* and *Theridiellum*.

Theridiella Tullgren, 1910, *in* Sjoestedt, Ergeb. Schwedischen Exped. Kilimandjaro, vol. 3, p. 136. Type species by monotypy: *T. monticola* Tullgren, 1910, *ibid.*, pl. 2, fig. 53, ♂, from Kilimanjaro, East Africa (NRS, examined). Synonym of *Coscinida.*

Theridiellum Dahl, 1912, Beitr. Naturdenkmalpflege, vol. 3, p. 598. Type species by monotypy: *T. minutissimum* Dahl, 1912, *ibid.*, ♀ ♂, from Europe (Berlin Museum) [= *Theonoe minutissima* (O.P.-Cambridge)]. Synonym of *Theonoe.*

[*Theridilella* Chamberlin and Ivie, 1936, Bull. Univ. Utah, biol. ser., vol. 3, no. 5, p. 33. Type species by original designation and monotypy: *T. zygops* Chamberlin and Ivie, 1936, *ibid.*, juv., from Panama (University of Utah Collection, examined). Synonym of *Theridiosoma,* transferred to Theridiosomatidae.]

Theridion Walckenaer, 1805, Tableau des Aranéides, p. 72. Type species designated by Int. Comm. Zool. Nomencl., Opinion 517, 1958: *Aranea picta* Walckenaer, 1802, Fauna Paris., vol. 2, p. 207, from Europe. *Theridion* is listed in the Official List of Generic Names in Zoology, name no. 1272. The subsequent invalid emendation: *Theridium* Leach, 1824, and *Theridio* Simon, 1864, are listed in the Official Index of Rejected and Invalid Generic Names in Zoology, names no. 1159, 1160, Opinion 517, 1958. Synonyms: *Neottiura, Tobesoa, ?Propostira, Phaetoticus, Wamba, Allodipoena, Allotheridion, Chindellum, Phylloncta, Nesticodes, Rugathodes,* and *Paidiscura.*

Theridiotis Levi, 1954, Trans. Amer. Micros. Soc., vol. 73, p. 178. Type species by original designation: *Dipoena jocosa* Gertsch and Davis, 1936, Amer. Mus. Novitates, no. 881, p. 7, fig. 20, ♀ ♂, from Texas (AMNH, examined). Synonym of *Chrosiothes.*

Theridula Emerton, 1882, Trans. Connecticut Acad. Sci., vol. 6, p. 25. Type species designated by Simon, 1894, Histoire Naturelle des Araignées, vol. 1, p. 551: *Theridion opulenta* Walckenaer. Emerton does not list *T. opulenta* and Simon apparently considered it a senior synonym of *T. sphaerula* (Hentz), which Emerton mentions. However, Emerton misidentified *T. sphaerula;* his specimens were *Theridula emertoni* Levi. *Theridion opulenta* (= *T. sphaerula*) is found in the southern United States. Synonym: *Mesopneustes.*

Tholocco Archer, "1946" [1947], Paper Alabama Mus. Nat. Hist., no. 22, p. 49. Type species by original designation: *Theridion amputatum* Keyserling, 1884, Die Spinnen Amerikas, Theridiidae, pt. 1, p. 90, pl. 4, fig. 58, from Florida [= *Thymoites unimaculatus* (Emerton)]. Synonym of *Thymoites.*

Thonastica Simon, 1908, Bull. Sci. France, Belgique, vol. 42, p. 92. Type species by monotypy: *T. praemollis* Simon, 1909, *ibid.*, ♀, from Tonkin (MNHN, examined). Synonym of *Thymoites.*

Thwaitesia O.P.-Cambridge, 1881, Proc. Zool. Soc. London, p. 766. Type species by monotypy: *T. margaritifera* O.P.-Cambridge, 1881, *op. cit.*,

p. 767, pl. 66, fig. 1, ♀ ♂, from Ceylon (HDE, examined). Synonyms: *Hildbolda, Topo.*

Thymoella Bryant, 1948, Bull. Mus. Comp. Zool., vol. 100, p. 377. Type species by original designation and monotypy: *T. banksi* Bryant, 1948, *op. cit.*, p. 378, figs. 58, 59, 62, 64, 65, 66, ♂ (MCZ, examined). Synonym of *Thymoites.*

Thymoites Keyserling, 1884, Die Spinnen Amerikas, Theridiidae, pt. 1, p. 161. Type species by monotypy: *T. crassipes* Keyserling, 1884, *op. cit.*, p. 162, ♂, from Peru (PAS, examined). Synonyms: *Sphyrotinus, Hypobares, Philto, Hubba, Thonastica, Garricola, Paidisca, Brontosauriella, Spelobion, Tholocco, Thymoella.*

Tidarren Chamberlin and Ivie, 1934, Bull. Univ. Utah, biol. ser., vol. 2, no. 4, p. 4. Type species by original designation: the nominal species *Theridion fordum* Keyserling, 1884, Die Spinnen Amerikas, Theridiidae, pt. 1, p. 23, tab. 1, fig. 9, from South America. [However, the specimens Chamberlin and Ivie considered *fordum* Keyserling were misidentified; they were *T. sisyphoides* (Walckenaer).]

Tobesoa Keyserling, 1890, *in* L. Koch, Die Arachniden Australiens, pt. 2, p. 239. Type species by monotypy: *T. theridioides* Keyserling, 1890, *op. cit.*, p. 240, pl. 21, fig. 6, ♀ ♂, from Australia. Synonym of *Theridion.*

Tomoxena Simon, 1894, Histoire Naturelle des Araignées, vol. 1, p. 518. Type species by original designation: *T. dives* Simon, 1895, Ann. Soc. Ent. France, vol. 64, p. 132, ♀, from India (MNHN, examined).

Topo Exline, 1950, Studies Honoring Trevor Kincaid, Univ. Washington Press, p. 113. Type species by original designation and monotypy: *T. bracteatus* Exline, 1950, *op. cit.*, p. 114, pl. 1, figs. 1, 6, pl. 2, fig. 15, ♀, from Ecuador (MCZ, examined). Synonym of *Thwaitesia.*

Tricantha Simon, 1864, Histoire Naturelle des Araignées, first edit., p. 293. Type species by monotypy: *T. tricornis* Simon, 1864, *op. cit.*, p. 293, ♀, from Brazil (MNHN, examined) [= *Trithena tricuspidata* (Blackwall)]. Synonym of *Phoroncidia.* [Thorell and others have changed the spelling of Simon's generic name to *Triacantha.*]

Trigonobothrys Simon, "1888" [1889], Ann. Soc. Ent. France, ser. 6, vol. 8, p. 230. Type species by monotypy: *T. excisus* Simon, 1888, *op. cit.*, p. 231, ♀, from Madagascar (MNHN, examined). Synonym of *Dipoena.*

Trithena Simon, 1867, Rev. Zool., p. 22. Type species by monotypy: *T. inuncans* Simon, 1867, *op. cit.*, p. 23, from Brazil (MNHN, examined) [= *T. tricuspidata* (Blackwall)]. Synonym of *Phoroncidia.*

[*Troglonata* Simon, 1922, Bull. Soc. Ent. France, p. 200. Type species by monotypy: *T. granulum* Simon, 1922, *ibid.*, ♀ ♂, from France (MNHN, examined). Transferred to Symphytognathidae.]

Ulesanis L. Koch, 1872, Die Arachniden Australiens, p. 242. Type species designated by Simon, 1894, Histoire Naturelle des Araignées, vol. 1, p. 560: *U. chelys* L. Koch, 1872, *op. cit.*, p. 244, pl. 20, fig. 4, ♀, from Samoa [= *U. personata* L. Koch]. Synonym of *Phoroncidia.*

Umfila Keyserling, 1886, Die Spinnen Amerikas, Theridiidae, pt. 2, p. 256. Type species by monotypy: *U. granulata* Keyserling, 1886, *op. cit.*, p. 257, from Brazil (types not in BMNH, probably lost, however, a ♂ in the MNHN, examined). Synonym of *Dipoena.*

[*Vibradellus* Chamberlin, 1925, Bull. Mus. Comp. Zool., vol. 67, p. 214. Type species by original designation and monotypy: *V. carolinus* Chamberlin, 1925, *ibid.*, p. 114, ♂ from the southern United States (MCZ, examined) [= *Gasteracantha cancriformis* (Linnaeus)]. Family Argiopidae.]

Wamba O.P.-Cambridge, 1896, Biologia Centrali-Americana, Araneidea, vol. 1, p. 190. Type species by monotypy: *W. congener* O.P.-Cambridge, 1896, *ibid.*, pl. 24, figs. 1a-f, ♂, from Guatemala (BMNH) [= *Theridion atropunctatum* Petrunkevitch]. Synonym of *Theridion.*

Wibrada Keyserling, 1886, Die Spinnen Amerikas, Theridiidae, pt. 2, p. 22. Type species by monotypy: *W. longiceps* Keyserling, 1886, *ibid.*, ♂, from Peru (MNHN, examined). Probably synonym of *Phoroncidia.*

Wirada Keyserling, 1886, Die Spinnen Amerikas, Theridiidae, pt. 2, p. 25. Type species by monotypy: *W. punctata* Keyserling, 1886, *op. cit.*, p. 26, ♂, from Peru (PAS, examined).

[*Zangherella* Caporiacco, 1949, Redia, Firenze, vol. 34, p. 259. Type species by monotypy: *Z. minima* Caporiacco, 1949, *op. cit.*, p. 260, fig. 4, ♂, from Castelraniero, Romagna, Italy (types lost, paratypes in the personal collection of Prof. P. Zangheri, examined). Transferred to Symphytognathidae.]

Key to Genera

In order to key species of theridiids to genus, specimens of both sexes are necessary. No characters are known that separate the females of *Coleosoma, Theridion,* and *Theridula,* for instance. On the other hand, the genera *Dipoena, Euryopis* and *Audifia* are easiest to separate from other genera by the number of seminal receptacles in the female (four subspherical in the mentioned genera, two in all other theridiid genera).

While new genera should not be described unless both sexes are known, many species will probably be described from only one sex. The only recommendation we can make is that these species temporarily be placed in the nearest genus, possibly the large genera, *Theridion, Anelosimus* or *Steatoda.*

It should be kept in mind that some genera, such as *Dipoena-Euryopis* and *Theridion-Thymoites, Styposis-Pholcomma, Steatoda-Enoplognatha,* intergrade, and the position of some species may be arbitrary, although the majority of species belonging to these genera can easily be placed. For this reason it has been necessary to use the unsatisfactory words "often" and "usually" in the key to differentiate these genera.

In this key, genera recognizable by non-genitalic characters (easy to observe) are separated first; genera that can be diagnosed only by genitalic characters, last. While this key includes all known theridiid genera, it should be possible to construct a much simpler key, using only non-genitalic characters, for the genera occurring in a limited region.

1a. Colulus always present, at least half as long as its setae (Figs. 3, 4) ..... Key C, p. 37

1b. Colulus absent (Fig. 1) or if present, then shorter than one-quarter length of its setae (Fig. 2) 2

2a. Colulus absent (Fig. 1) ..... Key A, p. 33

2b. Colulus present, or colulus replaced by two setae (Fig. 2) ..... Key B, p. 35

Key A (theridiids without colulus)

1a. Carapace, sternum with scattered tubercles (Fig. 250); selerotized ring around spinnerets hiding colulus setae ..... *Wirada*

1b. Carapace, sternum without tubercles 2

2a. Eye region of carapace projecting above clypeus (Figs. 238, 244); abdomen heavily sclerotized, usually with folds or spines (Figs. 235, 244, 247); sclerotized ring around spinnerets hiding the two colulus setae ..... *Phoroncidia*

2b. Eye region of carapace not projecting, or if projecting, abdomen not heavily sclerotized with folds or spines 3

3a. Carapace bulging anteriorly (Fig. 178); abdomen with posterior tubercles (Figs. 178, 183); palpus with an extra selerite (Figs. 181, 182); Ceylon ..... *Cephalobares*

3b. Carapace and abdomen not as above; palpus without extra selerite .. 4

4a. Abdomen higher than long with 3 large spines and a sclerotized ring around spinnerets (Fig. 134) [♂ unknown]; Ceylon to Singapore ..... *Molione*

4b. Abdomen otherwise 5

5a. Cephalothorax with a short posterior stalk (Fig. 174), abdomen oval in outline; male embolus and female connecting ducts short (Figs. 172, 175, 176); Brazil ..... *Hetschkia*

5b. Cephalothorax otherwise; or if similar, abdomen extended beyond spinnerets, embolus and connecting ducts long, male conductor S-shaped 6

6a. Cephalothorax modified, flat oval or with posterior stalk (Figs. 160, 163, 167); abdomen extended beyond spinnerets and a sclerotized ring around pedicel (Fig. 168); male embolus and female connecting ducts very long and threadlike (Figs. 161, 165, 166); tropical America ..... *Helvibis*

6b. Cephalothorax and abdomen otherwise 7

7a. Femur I of male with thorn below (Fig. 86); carapace low and long, abdomen much longer than wide (Figs. 85, 86); Samoa .. *Cyllognatha*

7b. Femur I of male without thorn on venter; carapace, abdomen otherwise 8

8a. Six eyes; or, with eight eyes but anterior medians with maximum diameter equal to radius of posterior medians (Fig. 231), and palpal bulb twisted with embolus facing outside (ectal) (Figs. 232, 233); Americas ..... *Styposis*

8b. Eight eyes; if anterior medians small, palpal bulb not facing ectal side 9

9a. Eyes of posterior row their diameter apart or less, eye region black (Figs. 144, 145), carapace low, male embolus with broad basal portion and a threadlike tube, radix present (Figs. 141, 148, 149), abdomen suboval, 1½ times longer than wide or high ..... *Coscinida*

9b. Posterior eyes their diameter or more apart; or, if eyes close together and large, eye region rarely black, and palpus or abdomen otherwise 10

10a. Females with four seminal receptacles (Figs. 34, 36) (except *Euryopis nana, E. argentea* and *E. saukea*), abdomen subtriangular (Figs. 29-31); palpus with duct looping through length of median apophysis, which is broadly attached to tegulum, radix absent (Figs. 32, 35) ..... *Euryopis*

10b. Females with two seminal receptacles, abdomen sometimes subtriangular, palpus with duct not looping through length of median apophysis when broadly attached to tegulum; radix present or absent 11

11a. Abdomen subtriangular, widest at anterior (Fig. 171) [♂ unknown]; India ..... *Tomoxena*

11b. Abdomen otherwise 12

12a. Carapace, sternum heavily sclerotized, abdomen with dorsal, posterior humps and characteristic spotted pattern (Figs. 155, 156, 159) ..... *Dipoenura*

12b. Carapace, sternum rarely heavily sclerotized; if sclerotized, abdomen otherwise 13

13a. Abdomen not sclerotized in either sex, with a single posterior, dorsal tip overhanging spinnerets, usually longer than high, often with grooves on sides (Figs. 108-111), male always with radix and separate median apophysis ..... *Chrysso*

13b. Abdomen otherwise; or, if with posterior dorsal tip overhanging spinnerets, male with anterior sclerotized ring on abdomen (*Coleosoma*); or lacking radix and having median apophysis broadly attached to tegulum or embolus (*Achaearanea*) 14

14a. One tooth on the posterior margin of chelicerae, palpus very simple without conductor, median apophysis, radix (Figs. 67, 68), abdomen suboval; America ..... *Paratheridula*

14b. Posterior margin without teeth, or if with a tooth, abdomen with a posterior dorsal extension (*Coleosoma*) 15

15a. Abdomen of male with a sclerotized ring around pedicel covering anterior half of venter, and abdomen sometimes constricted in middle (Figs. 105, 106), male embolus with a broad basal portion and a long

tube (Figs. 103, 104, 107) ..... *Coleosoma*

15b. Abdomen of male without sclerotized ring, or if with sclerotized ring venter not covered, and abdomen not constricted 16

16a. Male with only one very large palpus (Fig. 87); female abdomen higher than long, with a white line from dorsal tip to anal tubercle (Fig. 89); epigynum with a pair of openings, one on each side of a cone-shaped knob; male less than ¼ length of female ..... *Tidarren*

16b. Male always with two palpi; female abdomen, if higher than long and with white line, then epigynum not a cone-shaped knob; male ½ length or more than female 17

17a. Male palpus with a coiled duct in tegulum; cymbium with a serrated tip (Fig. 72); seemingly without radix, median apophysis or conductor; abdomen oval; less than 2 mm total length; South Africa ..... *Histagonia*

17b. Palpus rarely with coiled duct; if with coiled duct, cymbium without serrated tip and with conductor 18

18a. Palpus without conductor; no median apophysis; tegulum attached to cymbium on both ends (Figs. 70, 71); female abdomen wider than long (Fig. 69) ..... *Theridula*

18b. Palpus with conductor; median apophysis a separate sclerite or a lobe of the tegulum; tegulum always attached to cymbium at proximal end only; female abdomen sometimes wider than long 19

19a. Median apophysis broadly attached to tegulum or to embolus, never a separate sclerite (Figs. 74, 76, 78); abdomen usually higher than long, often with dark patches on sides (Figs. 79, 80), sometimes with a posterior dorsal tubercle (Fig. 81); palpus without radix ..... *Achaearanea*

19b. Median apophysis always a separate sclerite; abdomen usually longer than high or suboval, never with a tubercle, palpus almost always with radix (Figs. 94, 95, 125) 20

20a. Less than 2.5 mm in total length, uniformly colored (except for discrete black spots or gray marks), first patella and tibia usually less than one and one-half times length of carapace. Eye region of males often with grotesque projection, elevated, sometimes clypeus with a transverse groove (Figs. 121-124, 132), abdomen sometimes heavily sclerotized ..... *Thymoites*

20b. Usually larger spiders, usually with pattern or band on abdomen containing white and black pigment, first patella and tibia usually longer; male carapace never grotesquely modified, abdomen never sclerotized (except for narrow sclerotized ring around pedicel in males of some species) ..... *Theridion*

Key B (theridiids with colulus shorter than one-quarter length of its setae or colulus replaced by two setae)

1a. Carapace, sternum with scattered tubercles (Fig. 250); South America ..... *Wirada*

1b. Carapace, sternum without tubercles 2

2a. Eye region of carapace projecting above clypeus (Figs. 235,244); abdomen heavily sclerotized, often folded or with spines (Figs. 235, 244, 247); female with two seminal receptacles; paracymbium usually a hook on margin of cymbium of male palpus (Fig. 245) ..... *Phoroncidia*

2b. Eye region not projecting (or if projecting, then four seminal receptacles and paracymbial hook on back of cymbium); abdomen not heavily sclerotized (or if sclerotized, oval in outline) 3

3a. Abdomen of both sexes extended, longer behind spinnerets than in front or worm-shaped (Fig. 304) ..... *Argyrodes*

3b. Abdomen barely overhanging spinnerets behind (Figs. 190, 201, 207) 4

4a. Cephalothorax stalked, stalk as long as ½ width of carapace (Fig. 189), and abdomen higher than long (Fig. 190); tropical America ..... *Cerocida*

4b. Cephalothorax without stalk, or if present stalk less than ¼ width of carapace and abdomen not higher than long 5

5a. Two pairs of round or oval seminal receptacles in female (Figs. 48, 58); male carapace often with dorsal grooves (Figs. 45-47); male palpus wth duct usually looping through median apophysis (Figs. 49-51); embolus, if long, pointing counterclockwise in left palpus (Fig. 57) 6

5b. One pair of round or oval seminal receptacles (sometimes thin-walled asymmetrical pockets present); male carapace never with dorsal grooves; male with duct rarely looping through length of median apophysis (*Spintharus*); embolus generally pointing clockwise in left palpus (Figs. 205, 215, 245, 248) 9

6a. Carapace elongated, widest in posterior portion (Fig. 63); abdomen with sclerotized rings around spinnerets and pedicel (Fig. 64); legs long [♂ unknown]; South America, Africa ..... *Audifia*

6b. Carapace not elongated, abdomen rarely with sclerotized rings; legs of medium length (first patella and tibia less than one and one-half times carapace length) 7

7a. Teeth on anterior margin of chelicerae, minute denticles on posterior margin; palpus with paracymbial hook on cymbium margin (Fig. 234) ..... *Pholcomma*

7b. Chelicerae without teeth; paracymbial hook not on cymbial margin 8

8a. Palpus without radix; median apophysis broadly attached to tegulum (Figs. 32, 35); abdomen subtriangular (Figs. 29, 30, 31); male carapace rarely different in shape from that of female ..... *Euryopis*

8b. Palpus with radix (Figs. 49, 50); or if not, median apophysis a separate sclerite (Fig. 51); abdomen usually subspherical, wider than long or with humps, rarely subtriangular (Figs. 40-43); carapace of male often high, cylindrical, with grooves on dorsum (Figs. 45-47) ..... *Dipoena*

9a. Six eyes; or if eight eyes, then maximum diameter of anterior medians equal to radius of posterior medians (Fig. 231) and palpal bulb twisted with embolus facing lateral (Figs. 232, 233) ..... *Styposis*

9b. Eight eyes; maximum diameter of anterior medians more than radius of posteriors; or if maximum diameter of anterior medians equal to radius of posteriors, palpal embolus facing venter 10

10a. Posterior median eyes farther from each other than from laterals or equally spaced, and not more than one-third their diameter from laterals (but usually touching) and carapace black in eye region (Fig. 188) ..... *Stemmops*

10b. Posterior eyes otherwise, or if similar, eye region of carapace not black 11

11a. Chelicerae without denticles or teeth on posterior margin; abdomen usually with humps, subtriangular or wider than long 12

11b. Chelicerae with denticles or teeth on posterior margin (Figs. 18, 19); abdomen usually ovoid 16

12a. Chelicerae without teeth, abdomen wider than long, palpus circular in outline (Figs. 196, 197); Americas ..... *Tekellina*

12b. Chelicerae with one or two teeth on anterior margin, palpus not circular in outline 13

13a. Embolus long, with tip supported by cymbium; conductor absent or minute (Figs. 199, 200); epigynum an indistinct depression with connecting ducts coiled on each side and seminal receptacles anterior (Fig. 198); abdomen black or dark on venter above pedicel (Figs. 201, 202); tropical America ..... *Chrosiothes*

13b. Embolus never supported by cymbium; conductor very large; epigynum otherwise; abdomen colored otherwise 14

14a. Abdomen widest at middle or posterior to middle (Figs. 220, 221, 228), never higher than wide; without silvery plates; lateral eyes often separated; eyes often on tubercles; usually tubercles or horns between anterior and posterior median eyes (Fig. 221) ..... *Episinus*

14b. Abdomen widest anterior to middle, or higher than wide sometimes with silvery plates (Figs. 203, 207); lateral eyes touching; eyes never on tubercles; no tubercles between eyes 15

15a. Posterior median eyes about their diameter or less apart (Fig. 211); abdomen covered by silvery plates (Figs. 207, 212) ..... *Thwaitesia*

15b. Posterior median eyes two to three diameters apart (Fig. 203); abdomen not covered by silvery plates (Figs. 203, 204) ..... *Spintharus*

16a. Abdomen of male (sometimes female) heavily sclerotized; abdomen uniformly colored or with some indistinct dark patches; paracymbial hook on cymbium margin (Fig. 234), less than 1.8 mm total length ..... *Pholcomma*

16b. Abdomen not sclerotized, often with a longitudinal, dorsal dark band (Fig. 184); paracymbial hook usually in alveolus of cymbium; more than 1.4 mm total length ..... *Anelosimus*

Key C (colulus always present, at least half as long as its setae)

1a. Comb on fourth tarsus absent (except in Nesticidae); paracymbium a separate sclerite (Linyphiidae) or a hook on proximal part of cymbium (Nesticidae, Argiopidae, Tetragnathidae, Theridiosomatidae); or spider minute in size, tarsi longer than metatarsi, palpi

relatively simple without paracymbium (Symphytognathidae). Cheliceral anterior and posterior margins with more than 3 subequal teeth (fewer in Nesticidae) and shape of chelicerae as in Figures 23-28; distal margin of labium swollen, rebordered ... *other related families*

1b. Comb on fourth tarsus usually present (except *Argyrodes*); paracymbium, if present, in alveolus of cymbium (Figs. 252, 302), or on margin of cymbium (Figs. 280, 291, 293) never proximal; metatarsi generally longer than tarsi (except *Comaroma, Theonoe*); chelicerae generally with 3 or fewer teeth on anterior margin, fewer than 3 teeth (longer than wide) on posterior margin unless they are minute denticles (as wide as long); shape of chelicerae as in Figures 9-22; distal margin of labium not swollen (rebordered) 2

2a. Chelicerae without teeth (Figs. 14, 15); lateral eyes always separated; embolus and connecting ducts of female coiled (Fig. 253); seminal receptacles dumbbell-shaped (Fig. 254) ..... *Latrodectus*

2b. Chelicerae with one or more teeth or denticles; lateral eyes sometimes separated; embolus, connecting ducts rarely coiled; seminal receptacles not dumbbell-shaped 3

3a. With 6 eyes; or if 8 eyes, then diameter of anterior medians minute (less than radius of laterals); abdomen with sclerotized spots or scuta; [small spiders, less than 2 mm in total length] .... *Comaroma*

3b. With 8 eyes, diameter of medians larger than radius of laterals 4

4a. With denticles or teeth on posterior margin of chelicerae 5

4b. Posterior margin of chelicerae lacking teeth or denticles 8

5a. Abdomen of both sexes usually modified with humps, or narrowly elongate to worm-shaped, or higher than long (Figs. 303-305); eye region of male usually with projections, male clypeus usually with projections, grooves or bulging (Figs. 299, 301) ..... *Argyrodes*

5b. Abdomen broadly rounded; male clypeus and eye region not modified as above 6

6a. Posterior margin on chelicerae with two denticles; palpal cymbium elongate, usually twice as wide proximally as distally (Figs. 290, 291); abdomen without marking ..... *Robertus*

6b. Posterior margin with one tooth in female, one in male, or male chelicerae enlarged with several teeth on posterior margin; palpal cymbium oval; abdomen white, spotted, or with a pattern 7

7a. Median apophysis large, paracymbium on cymbium margin (Fig. 282); chelicerae of male enlarged (Fig. 281), sclerotized; usually dark in color, abdomen with a dorsal pattern ..... *Enoplognatha*

7b. Median apophysis minute, paracymbium not hook-shaped (Figs. 286, 289), chelicerae of male not enlarged; white in color, soft, very lightly sclerotized; New Zealand ..... *Icona*

8a. Sclerotized ring or plates on female abdomen around pedicel; cymbium with a spur (Figs. 273, 274) or male clypeus with a hook (Fig. 278) 9

8b. No sclerotized ring on female abdomen; cymbium without spur, male clypeus without a hook 10

9a. Clypeus of male bearing a fleshy hook (Fig. 278), cymbium without spur; tropical America ..... *Craspedisia*

9b. Clypeus of male without such a hook, cymbium with a spur (Figs. 273, 274); Europe, North America ..... *Crustulina*

10a. Abdomen of both sexes higher than long, or with tubercles, or narrowly elongate to worm-shaped extending beyond spinnerets 11

10b. Abdomen suboval in outline, longer than wide or high 12

11a. Male palpal patella without a spur; male clypeus and eye region usually modified with projections or grooves (Figs. 299, 301) ..... *Argyrodes*

11b. Male palpal patella with a spur (Fig. 298); male clypeus and eye region not so modified ..... *Synotaxus*

12a. Tarsi longer than metatarsi; radix absent, median apophysis fused to embolus (Fig. 252); less than 1.5 mm total length; abdomen unicolor; Europe, North America ..... *Theonoe*

12b. Metatarsi longer than tarsi; radix present, median apophysis a separate sclerite; usually more than 2 mm total length; abdomen often purplish black with a white line around anterior, and other marking 13

13a. Male palpal tibia with a large hook (Fig. 333); Australia ..... *Nicodamus* (Zodariidae)

13b. Male palpal tibia without a large hook ..... *Steatoda*

Descriptions and Diagnoses of Theridiid Genera

A. Theridiids with two pairs of seminal receptacles in female.

Euryopis Menge

Figures 9, 10, 29-39

Carapace variable in shape, sometimes head region high. Posterior median eyes their diameter or more apart. Chelicerae very small, lacking teeth; fang long and flattened (Figs. 9, 10). Leg IV usually slightly longer than I; leg III may be longer than II; patella and tibia IV, 1 to 1.7 times length of carapace. Abdomen usually triangular, pointed behind (Figs. 29-31), sometimes sclerotized with scuta in males (Fig. 33), often with silver spots or marks on dorsum. Colulus absent or replaced by two small setae.

Four seminal receptacles in female (Figs. 34, 36, 37) [Except in *E. argentea* Emerton, *E. saukea* Levi and *E. nana* (O.P.-Cambridge) whose males have a *Euryopis* palpus]. Palpus without radix; median apophysis broadly attached to tegulum (sometimes with a seam) and with duct looping through it (Figs. 32, 35).

Separated from most genera by presence of four seminal receptacles (with some exceptions); from *Dipoena* by lack of radix, the attachment of the median apophysis to the tegulum, the triangular abdomen (only rarely triangular in *Dipoena*), and often by lacking the setae that replace the colulus. The two genera probably intergrade. Males are distinct from *Stemmops* and *Coscinida* in not having the left embolus long and pointing clockwise, and in having the duct loop through the median apophysis. The species having the simplest palpus may be related to the genus *Achaearanea*. Three species [*E. argentea* Emerton, *E. nana* (O.P.-Cambridge), and *E. saukea* Levi] have only one pair of seminal receptacles. Other similarities to *Achaearanea* are that the cymbium extends beyond the alveolus and that the median apophysis is a lobe of the tegulum. *Achaearanea* differs, however, in that the duct does not go through the median apophysis.

Cosmopolitan, probably all ant feeders.

Both *Atkinsonia nana* O.P.-Cambridge (Figs. 38, 39) and *Acanthomysmena spinifera* Mello-Leitão are closely allied to *E. spinigera* O.P.-Cambridge. No characters are known that separate *Diaprocorus multipunctatus* Simon (Fig. 37) and *Phycosoma oecobioides* O.P.-Cambridge from *Euryopis*. *Phylarchus brevis* (O.P.-Cambridge), described from a juvenile, is closely allied to *E. taczanowskii* Keyserling [=*Euryopis nigripes* Banks] (Fig. 29) or may be the same.

Dipoena Thorell

Figures 11, 12, 40-62

Male carapace often very high, sometimes as high as long, cylindrical with dorsal grooves or depressions (Figs. 45-47), or in some species low, like that of female (Fig. 44). Carapace of female only rarely modified by being high. Eye region often slightly projecting above clypeus. Anterior median eyes sometimes larger than others; however, this is not a diagnostic character as the eyes are often subequal in size and species of other genera may have the anterior medians large. Posterior median eyes usually their diameter or less apart. Clypeus often concave. Chelicerae very small without teeth; fang long and flat (Figs. 11, 12). Legs I or IV slightly the longest. Longest patella-tibia 1 to 2 times length of carapace. Abdomen often modified, sometimes wider than long, heart-shaped or higher than long, sometimes sclerotized with a dorsal scutum or with humps (Figs.

40-43). Abdomen sometimes dark reddish in color. Related species often differ in coloration and shape of abdomen. Colulus replaced by two setae.

Female with four seminal receptacles (Fig. 48); ducts ventral to receptacles, so that the cleared epigynum is more diagnostic than is the dorsal view of the seminal receptacles. Palpus with median apophysis often attached to tegulum, ducts looping through it. Radix usually present; if absent, median apophysis a separate sclerite. Duct long, looping through median apophysis, often taking a tortuous course through tegulum (Figs. 49-51). Left embolus, if long, usually pointing counterclockwise.

Separated from most theridiid genera by having four subequal seminal receptacles in female. Separated from *Euryopis* by having a radix, or if radix is absent, by having median apophysis a separate sclerite; sometimes by having a more winding duct in the tegulum; and always by having the colulus replaced by two setae. The high carapace of males readily separates many species of *Dipoena,* as such carapace modification is unknown in other genera.

Cosmopolitan. Probably all feed on ants.

Umfila granulata Keyserling superficially resembles *Euryopis spinigera* O.P.-Cambridge; however, the carapace has grooves (Fig. 55), and the palpus is complex; the cymbium is modified and the nonfunctional median apophysis has moved to a proximal position (Fig. 57). *Paoningia turriceps* Schenkel (Fig. 62) has a high *Dipoena* carapace illustrated by Schenkel. *Stictoxena sertata* Simon (Figs. 60, 61) is probably *Dipoena* although the embolus resembles that of *Theridion.* The median apophysis and radix are fused (Fig. 61). *Trigonobothrys excisus* Simon is a *Dipoena;* the female (Fig. 54) and male (Figs. 52, 53) do not belong together. The palpus resembles that of the American *Dipoena alta* Keyserling; it might be the same species although the dorsal abdominal scutum of *D. alta* is flat, and that of *T. excisus* has humps (Fig. 52). Hickman (1951, Papers Proc. Roy. Soc. Tasmania, 1950; pp. 3-24) placed the genera *Trigonobothrys* and *Atkinsonia* close to *Ulesanis* [*Phoroncidia*] because of the sclerotized ring around the spinnerets and the heavy sclerotization. His excellent drawings however, show that *Trigonobothrys* is a *Dipoena,* and *Atkinsonia* is a *Euryopis.* Hickman apparently did not realize that heavy sclerotization may be found in groups other than those allied to *Phoroncidia.*

Audifia Keyserling

Figures 63-66

Carapace and sternum elongate (Figs. 63, 64). Chelicerae very small, probably without teeth. Abdomen with sclerotized ring around spinnerets, and sclerotized pedicel (Fig. 64). Colulus replaced by two setae.

Four seminal receptacles in female (Fig. 65). Male unknown.

Separated from *Dipoena* by elongate prosoma, from *Phoroncidia* by its longer legs and by having four seminal receptacles.

Females of three species known, two from South America, one from the Congo.

B. Theridiids with one pair of seminal receptacles in female, and lacking colulus.

Paratheridula Levi

Figures 67, 68

Carapace as in *Theridion*, not modified. Chelicerae with two teeth on anterior margin, one of them compound; a small tooth on posterior margin in female. Leg I longest; first patella-tibia 1.3 to 1.4 times length of carapace. Abdomen subspherical. No colulus.

Palpus very simple; conductor, median apophysis, radix absent (Figs. 67, 68).

Separated from *Theridula* male by absence of distal haematodocha in palpus, from *Theridion* male by simple palpus. Small tooth on posterior margin of chelicerae separates the female from *Theridion* and allied genera.

Only one species known, widespread in warm parts of America.

Theridula Emerton

Figures 69-71

Carapace as in *Theridion*, not modified. Chelicerae with two teeth on anterior margin, none posterior. Leg I longest; patella-tibia 1.2 to 1.5 times length of carapace. Abdomen wider than long (Fig. 69). No colulus.

Palpus very simple, conductor, median apophysis, radix absent. Haematodocha fastens both ends of tegulum to the cymbium (Fig. 71).

Females may be difficult to separate from groups of *Theridion* that have abdomen wider than long. Separated from *Paratheridula* and *Theridion* males by the structure of the palpus. In no other theridiid genus is there a distal haematodocha.

Several similar species in all warm regions and eastern North America.

Histagonia Simon

Figures 72, 73

Carapace as in *Theridion*, not modified. Chelicerae small; fang half length of basal segment. Legs of medium length. Abdomen subspherical, not modified. Colulus probably absent. Very small in size.

Female with two seminal receptacles. Palpus with series of teeth on tip of cymbium; cymbium extending beyond alveolus. Embolus with coiled tip, duct coiled, probably no median apophysis; radix absent (Fig. 72). (As the only specimen had one palpus, its examination was superficial.)

Separated from *Achaearanea* by coiled duct in male palpus.

Probably this is a good genus, but a careful anatomical study of the palpus may reveal synonymy of this genus with *Achaearanea*.

Only one species known, from South Africa.

Achaearanea Strand

Figures 74-81

Carapace as in *Theridion*, not modified. Chelicerae without teeth, or rarely with a small tooth, sometimes a small keel, on anterior margin. Labium variable in shape, never separated from sternum. Leg I longest; first patella-tibia 1.2 to 2.5 times length of carapace. Abdomen usually higher than long; sometimes with one hump, rarely two; sometimes longer than wide or high. Abdomen often with a characteristic pattern of irregular streaks on sides (Figs. 79, 80), sometimes with the posterior portion white (Fig. 81). No colulus. Small to very large in size (1-10 mm total length). Males slightly smaller than females or of equal size.

Epigynum often a knob or depression. Palpus with tegulum spherical, median apophysis broadly attached to tegulum or attached to embolus with which it forms one sclerite (Figs. 74,

76, 77, 78). Radix absent. Cymbium often extending beyond alveolus.

Separated from *Theridion, Chrysso,* and *Tidarren* by palpal structure, lack of radix, and broad attachment of median apophysis to the tegulum or embolus. Females may be difficult to place, but in most species the high abdomen and characteristic streaky patterns suggest *Achaearanea.*

Cosmopolitan.

Dipoenura pyramidalis Simon may be the same as *Achaearanea conigera* (Simon) (Fig. 81), a southern European species known only from juvenile specimens.

Cyllognatha L. Koch

Figures 82-86

Carapace flat and long. Male chelicerae very strong, slightly elongate with one large tooth on anterior margin. Legs very long, leg I longest. Venter of femur I of male with thorns (Fig. 86). Abdomen much longer than wide, that of male with sclerotized ring around pedicel (Fig. 86). No colulus.

Palpus probably without radix; cymbium extended beyond alveolus. The palpus (Fig. 82) resembles (?superficially) that of *Theridion atropunctatum* Petrunkevitch.

Separated from *Theridion, Colcosoma* and other genera by ventral thorns of femora I of male, and by long abdomen. No characters are known that separate females from *Theridion* and *Coleosoma.*

Several species from Samoa.

Tidarren Chamberlin and Ivie

Figures 87-89

Carapace as in *Theridion,* not modified. Chelicerae without teeth or with one on anterior margin, none posterior. Male with only one palpus. Leg I longest, first patella-tibia 1.4 to 1.6 times carapace length. Abdomen higher than long, sometimes with a tubercle on posterior dorsal tip; sides streaked; a white posterior line from tip to spinnerets (Fig. 89). No colulus. Total length of females 2.5 to 6.0 times that of male.

Epigynum a projecting knob. Only one large palpus [the other palpus is removed by spider on becoming mature]. Palpus (Fig. 88) with radix, median apophysis and very large conductor; cymbium irregularly shaped, extending beyond alveolus.

Separated from *Achaearanea* by having a radix and free

median apophysis in the palpus, and by having only one palpus in adult males. The high abdomen with streaky marks and white stripe will separate females from *Theridion* and other genera (except *Achaearanea*).

Several similar species from warmer parts of America and Africa.

Theridion Walckenaer

Figures 1, 16, 17, 90-102

Carapace not modified. Chelicerae with no teeth, one or two teeth on anterior margin, none posterior (Figs. 16, 17); chelicerae sometimes elongate in males. Legs usually long; leg I longest, first patella-tibia 1.5 to 3 times carapace length. Abdomen usually suboval or subspherical (Fig. 93), sometimes wider than long. Male abdomen sometimes with a narrow anterior sclerotized ring around pedicel. No colulus.

Epigynum of various shapes. Palpus has all sclerites present (Figs. 94, 95).

Separated from *Chrysso, Coleosoma, Tidarren, Achaearanea* by having the abdomen suboval, subspherical, sometimes wider than long; from *Achaearanea* and *Tidarren* by having the cymbium only rarely extended beyond the alveolus; from *Achaearanea* by having a radix (only rarely secondarily absent) and a free median apophysis in the palpus; from *Tidarren* by having two palpi; and from *Thymoites* by larger size, longer legs and by never having the eye region of the carapace modified. It is difficult to recognize unaccompanied females of *Theridion* and related genera lacking the colulus, and the placement of some species in *Theridion* or *Thymoites* is arbitrary.

Cosmopolitan. Probably several hundred species.

Neottiura bimaculata (Linnaeus) is tentatively considered to belong to *Theridion*, despite having a retrolateral thorn on femur IV of the male and a modified palpal cymbium. *Theridion suaveolus* Simon bridges the gap between other *Theridion* and *Neottiura bimaculata*. *Tobesoa theridioides* Keyserling (Figs. 100-102) is a *Theridion*. *Propostira quadrangulata* Simon (Figs. 96, 97) is known only from a female and is probably a *Theridion* although it might belong to *Achaearanea*. *Phactoticus modestus* Simon (Figs. 98, 99), in spite of relatively short thick legs, with first patella-tibia slightly longer than carapace, probably belongs to *Theridion;* the duct of the female internal genitalia loops anterior to the seminal receptacles (Fig. 98).

Coleosoma O.P.-Cambridge

Figures 103-107

Carapace of females as in *Theridion,* not modified; that of male oval with projecting clypeus. Chelicerae small, without teeth or with one or two teeth on anterior margin; none posterior, except that female of *C. acutiventer* Keyserling has one large tooth posterior. Leg I longest; first patella-tibia about 1.5 times carapace length. Female abdomen suboval or with a tubercle above and posterior to spinnerets as in *Chrysso.* Male abdomen sometimes constricted in middle. Anterior of male abdomen always has a sclerotized ring covering anterior half of venter (Figs. 105, 106), with a carina above. No colulus.

Epigynum lightly sclerotized, consisting of indistinct slits or a depression. Palpus with all sclerites present as in *Theridion;* embolus prominent on venter, left one pointing clockwise (Figs. 103, 104, 107).

Separated from *Theridion* by oval, projecting clypeus of male and by sclerotized ring around anterior of abdomen and half of venter. No characters are known that separate females from *Theridion* or *Chrysso.*

Cosmotropical; four species known.

Chrysso O.P.-Cambridge

Figures 22, 108-117

Carapace as in *Theridion,* not modified. Chelicerae with no teeth or one to three teeth on anterior margin, none posterior or sometimes several small teeth (Fig. 22), e.g. *Chrysso elegans* (Taczanowski) [= *Chrysso albomaculata* O.P.-Cambridge]. Legs often very long, leg I longer than IV; first patella-tibia 1.2 to 5 times carapace length. Abdomen usually longer than wide or high, very rarely higher than long, with a tubercle or tip above and posterior to spinnerets; sometimes furrows on sides (Figs. 108-111). No colulus. Often brightly colored with patches of black and white in alcoholic specimens.

Epigynum often with openings indistinct; sacs or connecting ducts joining openings and seminal receptacles. Palpus with cymbium often shallow, variously shaped; paracymbial hook indistinct. Median apophysis and radix separate sclerites.

Separated from *Theridion* by shape of abdomen; from *Achaearanea* by having a radix and free median apophysis in the

palpus, and usually also by the shape of the abdomen; from *Coleosoma* by lacking the anterior sclerotized ring around the male abdomen.

Known from Asia and Americas.

The species placed in *Chrysso* are quite diverse. The type species and others close to it have been illustrated in Levi, "1955" [1957]. It is not known whether the species placed in this genus are monophyletic. The common occurrence of modifications in the cymbium (rare in *Theridion*), suggests that members of the group, despite variously shaped palpi, are closely related. *Meotipa* is synonymized; the type *M. picturata* Simon is known only from a female (Figs. 112, 113). It has one tooth on the anterior margin of the chelicerae, long maxillae and the abdomen looks like that of *M. clementinae* Petrunkevitch (Fig. 110). *Physcoa scintillans,* known from a female, probably belongs to this genus. The genitalia (Figs. 116, 117) are similar to those of *C. indicifer* Chamberlin and Ivie. *Arctachaea* Levi is also included in *Chrysso* because of several intermediate species, illustrated in a paper in preparation.

Thymoites Keyserling

Figures 118-133

Eye region of males of most species (not all) bulging or projecting, sometimes with a seam between eyes or on clypeus below eyes (Figs. 121-124, 132); carapace of female not modified. Chelicerae with one tooth on anterior margin, none posterior. Legs usually short, leg I or IV longest; the longest patella-tibia 0.9 to 1.8 times length of carapace. Abdomen suboval, sometimes with ventral and dorsal sclerotized plates in males. No colulus. Color often brownish, orange or yellow-brown, without pattern, except sometimes a dusky, indistinct, longitudinal band on dorsum of abdomen, or discrete black spots. Usually less than 2.5 mm, most species less than 1.5 mm total length.

Openings of epigynum often indistinct but transparent epigynum shows some ducts (Fig. 119). Palpus with all sclerites present, or radix sometimes reduced or absent (Fig. 125).

Separated from other small theridiids by lack of colulus; from *Theridion* by having male carapace often modified, male abdomen sometimes sclerotized, relatively short legs, small size, yellowish color and by lacking a pattern on dorsum of abdomen. Some species probably intergrade with *Theridion* and are thus difficult to place.

Probably world-wide in warm regions.

Several genera of small theridiids are here considered synonyms of *Thymoites* because no characters are known to differentiate them. While the synonymy of *Sphyrotinus*, *Paidisca* and *Brontosauriella* (Figs. 131, 132) is in no doubt, the types of several other genera are known from only one sex. *Hypobares unisignatus* Simon (Figs. 128-130) belongs in this genus, as does *Philto subtilis* Simon (Fig. 133). *Thonastica praemollis* Simon (Figs. 126, 127) probably belongs here, but is known only from a female.

Molione Thorell

Figures 134-138

Carapace as in *Theridion*, not modified. Chelicerae as long as carapace is high, probably with two teeth on anterior margin. Abdomen higher than long, with three large dorsal, lightly sclerotized spines and a sclerotized ring around spinnerets (Figs. 134-136). Colulus absent.

Epigynum sclerotized with openings indistinct (Fig. 138).

Separated from *Theridion* by spines on abdomen and sclerotized ring around spinnerets.

Only females of two species known, from Singapore and Ceylon.

Coscinida Simon

Figures 139-149

Carapace as in *Theridion* but eyes very large, close together; posterior medians separated by their diameter or less (Figs. 144, 145), closer to laterals than to each other. Eye region black (Figs. 144, 145). Leg IV longest; fourth patella-tibia 1.2 to 1.7 times carapace length. Abdomen longer than wide or high. No colulus. Often gray abdomen has a white spot above spinnerets.

Walls of female connecting ducts sclerotized (Figs. 139, 146). Palpus with all sclerites present; embolus on ventral side, pointing clockwise in left palpus (Figs. 141, 148, 149).

Separated from other genera by large eyes, relatively close together; from *Stemmops* by lacking colulus; from *Theridion* by the longer, flatter abdomen and thicker legs.

In warm parts of Africa and America.

It is uncertain whether a single character (absence of colulus) warrants keeping the genus distinct from *Stemmops*.

Theridiella monticola Tullgren (Fig. 149) is the same species as *Loxonychia lugubris* Tullgren (Figs. 146-148). The type specimen of the former has the palpus expanded (Fig. 149). It belongs to the genus *Coscinida*.

Dipoenura Simon

Figures 150-159

Carapace, sternum sclerotized. Chelicerae small with one blunt tooth on anterior margin. Abdomen extended beyond and above spinnerets with four tubercles at posterior tip (Figs. 155, 156, 159). Colulus probably absent.

Epigyna of two species examined have openings in a central depression (Figs. 151, 158). Palpus with functional median apophysis, radix, conductor; embolus in part supported by tegulum and subtegulum (Fig. 154).

Separated from *Thymoites* by shape and coloration of abdomen and by the structure of the palpus; from *Argyrodes* by lack of colulus.

From Indochina, Africa; there are three species, two of which are illustrated, *D. fimbriata* Simon (Figs. 150-156) and *D. cyclosoides* (Simon) (Figs. 157-159). *Dipoenura pyramidalis* (Simon) probably belongs to the genus *Archaearanea,* and is known only from juveniles; the available name would be *A. conigera* (Simon) (Fig. 81).

Helvibis Keyserling

Figures 160-168

Carapace heavily sclerotized, suboval (Figs. 160, 163), of various shapes sometimes with posterior extension or stalk. Chelicerae small with a compound tooth on anterior margin, none posterior. Legs very long, first patella-tibia 1 to 2 times length of carapace. Tarsal comb may be absent. Abdomen extended beyond spinnerets; male with a sclerotized ring around pedicel. No colulus.

Connecting ducts of female very long, tortuous, and difficult to follow (Fig. 161). Palpus contains all sclerites; threadlike embolus very long (Fig. 166), supported by S-shaped conductor. Cymbium extending beyond alveolus.

Separated from *Theridion* by shape of carapace and extension of abdomen beyond spinnerets; from *Audifia* by having only two

seminal receptaeles and lacking colulus; from *Hetschkia* by structure of palpus; from *Chrysso* by modified carapace, and by having a sclerotized ring around anterior end of abdomen in males.

Known only from tropical America.

Species placed by Keyserling in *Formicinoides* have similar genitalia but a slightly different carapace shape (Figs. 167, 168). Various species of *Helvibis* differ more in carapace shape than in genitalia; the genitalia are similar in all species.

Tomoxena Simon

Figures 169-171

Carapace almost circular. Probably no teeth on chelicerae. Legs very long, first patella-tibia 3 times length of carapace. Leg IV longer than I. Abdomen subtriangular, widest anteriorly, with silvery spots (Fig. 171). Colulus absent.

Two seminal receptacles in female with ducts winding around them (Fig. 169); male unknown.

Separated from *Chrysso* and *Theridion* by the shape of the abdomen and by having fourth legs longer than first; from *Spintharus* by lacking colulus; from *Euryopis* by having only one pair of seminal receptacles. It is possible, however, that *Tomoxena* is an exceptional species of *Euryopis*, with only one pair of receptacles.

Two species from India and Sumatra.

Hetschkia Keyserling

Figures 172-177

Carapace sclerotized, suboval with a posterior stalk in both sexes (Fig. 174). Chelicerae probably with two teeth on anterior margin. Abdomen oval in outline. No colulus.

Palpus contains all sclerites; paracymbial hook near ectal margin of cymbium (Figs. 175-177).

Separated from *Theridion* by carapace shape; from *Helvibis* by having a short embolus and conductor and by suboval abdomen.

Only one species known, from Brazil.

Cephalobares O.P.-Cambridge

Figures 178-183

Anterior part of carapace enormously swollen in both sexes (Fig. 178). Chelicerae very small. Abdomen longer than wide;

extended beyond spinnerets; with posterior tubercles (Fig. 178). No colulus.

Two seminal receptacles. Palpus contains all the usual sclerites and apparently an additional one (Figs. 181, 182).

Separated from *Thymoites* by shape of abdomen, from other genera by carapace shape or lack of colulus, or both.

Only one species known, from Ceylon.

C. Theridiids with one pair of seminal receptacles in female, colulus replaced by two setae.

Anelosimus Simon

Figures 18, 19, 184, 185

Carapace as in *Theridion,* lightly sclerotized and not modified, but often elongate or pear-shaped (Fig. 184). Chelicerae with several teeth on anterior margin, 2 to 5 denticles posterior (Fig. 18). Leg I longest, first patella-tibia 1 to 2 times carapace length. Abdomen suboval, often slightly elongate, and often with dark median dorsal stripe [except for *A. attritus* (Nicolet) whose abdomen is subtriangular with two humps, side by side]. Colulus replaced by two setae.

Epigynum often with transverse folds; seminal receptacles often small; connecting ducts usually thin walled, sac-like. Palpus with all sclerites present, median apophysis inconspicuous, elongate in all species known (Fig. 185).

Separated from *Theridion* by having two setae replacing colulus and by cheliceral teeth.

Cosmopolitan.

Stemmops O.P.-Cambridge

Figures 186-188

Carapace as in *Theridion*, lightly sclerotized and not modified except eyes very large, close together. Posterior eyes equally spaced or closer to laterals, posterior medians touching or less than ⅓ their diameter from laterals. Anterior median eyes usually smaller than posterior medians (Fig. 188). Eye region black, except between posterior medians. Chelicerae small, probably without teeth. Leg IV longer than I, fourth patella-tibia 1.5 to 1.6 times carapace length. Abdomen slightly flattened, longer than wide. Colulus replaced by two short setae. Abdomen often with a white spot above spinnerets on uniform gray (Fig. 188).

Walls of female connecting ducts sclerotized. Palpus complex, with all sclerites present (Fig. 187).

Separated from other genera by large eyes, relatively close together, and short stout legs; from *Euryopis* by having only two seminal receptacles in female; from *Coscinida* by having colulus replaced by two setae.

In warm parts of America.

It is uncertain whether splitting the species into *Stemmops* and *Coscinida* on the basis of only one character, the colulus setae, is warranted. Better judgment can be made after more species are available for study.

Cerocida Simon

Figures 189-195

Cephalothorax selerotized with posterior stalk and raised reticulate pattern in both male and female (Fig. 189). Chelicerae small, probably without teeth. Legs long, the first patella-tibia as long as or slightly longer than carapace. Abdomen small, higher than long; male with sclerotized ring around pedicel and ring around spinnerets (Figs. 189, 190). Colulus replaced by two setae.

Seminal receptacles with long duct wrapped around them (Fig. 194). Palpus with embolus long, probably all selerites present. The translucent palpus with its large haematodocha is difficult to study (Figs. 191-193).

Separated from *Helvibis* by presence of colulus setae; from *Styposis* by having the palpal embolus facing ventrally.

Only one species known, from Venezuela, Guianas.

Tekellina Levi

Figures 196, 197

Carapace as in *Theridion,* weakly sclerotized and not modified. Chelicerae lacking teeth. Leg I longer than IV; first patella-tibia 1.6 times length of carapace. Abdomen wider than long. Colulus replaced by two setae. Small spiders, less than 1.3 mm total length.

Palpus with end of median apophysis lying against paracymbial hook near margin of cymbium. Cymbium almost circular (Fig. 196).

Separated from symphytognathids by having a colulus replaced by two setae and by absence of teeth on chelicerae; from other small theridiids by structure of palpus (Fig. 197).

Only one species known, from Florida.

Chrosiothes Simon

Figures 198-202

Carapace weakly sclerotized, sometimes highest in thoracic region, often with a wide black band, eyes with red pigment. Posterior eyes equally spaced or sometimes slightly closer to each other than to laterals; their radius or more apart. Chelicerae without teeth. Legs sometimes rather heavy, first or fourth leg longest. Longest patella-tibia 1 to 1.7 times carapace length. Abdomen variously shaped, subtriangular, suboval, or with a hump on each side; rarely oval in outline; usually with venter black, particularly area overhanging pedicel (Figs. 201, 202). Colulus replaced by two setae. Total length of male less than two-thirds total length of female.

Epigynum with an oval depression. Connecting duct of female forming a pair of coils posterior to seminal receptacles (Fig. 198). Palpus with conductor absent or minute. Cymbium modified to support tip of long embolus. Radix and median apophysis present (Figs. 199, 200). Median apophysis may be broadly attached to tegulum.

The cymbium (supporting embolus), absence of conductor, coiled connecting ducts, and coloration are diagnostic and separate this genus from *Episinus* and *Spintharus*, which also have the abdomen variously shaped. Unaccompanied females with the abdomen oval are, except for coloration, difficult to separate from *Anelosimus*.

Known only from warm parts of America.

The species of this genus, when revised, were placed in *Theridiotis* Levi (1954). *Theridiotis probabilis* (O.P.-Cambridge) is a synonym of *C. silvaticus* Simon.

Spintharus Hentz

Figures 203-206

Carapace nearly circular. Posterior median eyes separated by about three diameters (Fig. 203). Chelicerae small. Legs long, first patella-tibia 1.5 to 3.0 times carapace length. Abdomen longer than wide, widest anterior to middle (Figs. 203, 204).

Colulus replaced by two setae. Anterior spinnerets each with a spigot (Fig. 217).

Palpus with all sclerites present (Fig. 206). Median apophysis broadly attached to tegulum, but separated by a seam. Duct looping through median apophysis.

Separated from *Argyrodes* by having two setae in place of colulus; from *Episinus* by different abdominal shape, by lacking tubercles in eye region and by having a simpler palpus; from *Thwaitesia* by lacking silvery spots and having posterior median eyes farther apart. *Spintharus* is close to both *Episinus* and *Thwaitesia*, and some species probably are intermediate.

Several species from the Americas.

Thwaitesia O.P.-Cambridge

Figures 13, 207-219

Carapace nearly circular (Fig. 211). Posterior median eyes separated by about their diameter or less. Chelicerae small, without teeth (Fig. 13). Legs long, first patella-tibia 2.0 to 3.5 times carapace length. Abdomen usually higher than wide (Figs. 207, 212) with silvery spots. Colulus replaced by two setae. Anterior spinnerets each with a spigot (Fig. 217).

Palpus with all sclerites present (Fig. 216).

Separated from *Argyrodes* by having two setae in place of colulus; from *Episinus* by different shape of abdomen, by lacking tubercles in the eye region and by simpler palpus. *Thwaitesia* differs from *Spintharus* by having the posterior median eyes closer together and having silvery plates covering the abdomen. *Thwaitesia* is close to *Spintharus* and *Episinus* and some species probably are intermediate. The genus may have to be fused with *Spintharus*.

Probably world-wide in tropics.

Hildbolda simoni Keyserling has the abdomen wider than high with silvery spots. The female genitalia (Figs. 218, 219) are similar to those of other species of *Thwaitesia*. *Topo bracteatus* Exline is very close to *T. affinis* O.P.-Cambridge.

Episinus Latreille

Figures 220-230

Carapace often with a pair of tubercles between anterior and posterior median eyes, often with a deep longitudinal thoracic depression (Figs. 220, 221). Eyes often on slight tubercles;

lateral eyes sometimes separated. Red pigment often in eye region. Chelicerae small with a tooth on anterior margin or no teeth. First leg longest; first patella-tibia 1.4 to 2.8 times carapace length. Abdomen flat, usually modified with humps or nipples, widest behind middle (Figs. 220, 221). Often light colored or with gray marks on abdomen. Colulus replaced by two setae. A tiny spigot on anterior spinnerets.

Palpus extremely complex, all structures proliferated and large, connected by large haematodocha.

The modified abdomen separates *Episinus* from other genera with colulus replaced by two setae; tubercles in eye region, the shape and color of the abdomen and complex palpus separates it from *Spintharus*.

Cosmopolitan, mainly in warmer areas.

Hyocrea implexa Simon (Fig. 226) is known only from an early instar juvenile that has the abdomen like other *Episinus*. The badly preserved female type of *Hyptimorpha mirabilis* Strand (Figs. 224, 225) has the eyes on tubercles and the clypeus projecting; it is probably *Episinus*. *Moneta spinigera* O.P.-Cambridge (Figs. 228-230) is an *Episinus*. *Penictis mucronata* Simon, described from a juvenile, is probably *Episinus;* the abdomen is widest in front and has a pair of humps in the middle. *Plocamis theridioides* Simon (Figs. 222, 223) has the coloration and shape of *Episinus;* the abdomen is widest at the posterior end.

Styposis Simon

Figures 231-233

Carapace as long as wide, sometimes longer than wide with a short posterior stalk, some species weakly sclerotized but sometimes heavily sclerotized with a raised reticulate pattern (Fig. 231). Six large eyes arranged in two groups of three touching each other, or eight eyes with anterior medians minute, their maximum diameter equal to radius of posterior medians. Chelicerae small with one or two compound teeth on anterior margin, none posterior. Leg I longer than IV, first patella-tibia 1.4 to 2.7 times carapace length. Abdomen soft, suboval, subspherical or wider than long. Colulus replaced by two setae slightly anterior of usual position, very hard to see. Except for eyes, pigmentless white in alcohol. Small spiders less than 1.8 mm total length.

Female genitalia with two seminal receptacles. Male palpus weakly sclerotized, parts translucent and hard to see. Bulb

twisted so that embolus faces outside (and is partly hidden by cymbium) and median apophysis faces ventrally (Figs. 232, 233).

Separated from *Thymoites, Cerocida* and *Theridion* by the number and size of eyes and by the structure of the palpus. *Pholcomma hirsuta* Emerton is intermediate with *Styposis* but has larger anterior median eyes, and denticles on the posterior cheliceral margin; its palpus is like that of *Styposis*. *Pholcomma gibbum* (Westring) has similar eyes, but a different palpus.

Warm parts of America.

Pholcomma Thorell

Figure 234

Cephalothorax often sclerotized. Eyes sometimes close together, posterior medians closer to laterals than to each other; anterior medians usually smallest. Chelicerae with 3 to 4 teeth on anterior margin, 2 to 4 minute denticles posterior. Legs short, longest patella-tibia equal to length of carapace or shorter. Metatarsi or tarsi of equal length or tarsi shorter. Tarsal comb on leg IV reduced or absent. Abdomen sometimes sclerotized in female, always in male, suboval in outline. Colulus replaced by two setae. Small spiders, less than 1.8 mm total length.

Sometimes ducts of female widened, forming additional seminal receptacles. Palpus with paracymbial hook on margin of cymbium. End of median apophysis not lying against paracymbial hook; tegulum tube-shaped rather than spherical (Fig. 234).

Separated from *Thymoites* and *Comaroma* by colulus setae; from *Stemmops* by smaller size, structure of chelicerae and sclerotized abdomen. *Pholcomma gibbum* (Westring) has eyes somewhat similar to those of *Styposis,* but the bulb of the palpus has the embolus on the venter. *Pholcomma hirsuta* Emerton has the bulb of the palpus twisted as in *Styposis,* but has larger anterior median eyes, and has denticles on the posterior cheliceral margin. *Pholcomma* and *Styposis* are probably closely related and some species may be intermediate.

Cosmopolitan.

The type species and North American species have been illustrated previously (Levi, 1957).

No characters that would separate *Armigera* Marples from *Pholcomma* were found in several specimens of *Armigera* examined.

Phoroncidia Westwood

Figures 235-247

Carapace with eye region projecting anteriorly, overhanging clypeus (Figs. 235, 244). Chelicerae small. Legs very short, leg IV longer than I. Abdomen heavily sclerotized, of various shapes; often leathery, folded, or with strong spines (Figs. 235, 244, 247). Sclerotized ring around spinnerets. Colulus replaced by two setae, often very difficult to see, hidden by sclerotized ring.

Epigynum a sclerotized plate with openings indistinct (Figs. 236, 246). Palpus with paracymbial hook on edge of cymbium, median apophysis probably not lying against it (Fig. 245).

Readily separated from other theridiid genera by shape and heavy sclerotization of abdomen, and projecting eye region of carapace.

Cosmopolitan, but absent from western North America and temperate Europe.

The specimens of *P. aculeata* Westwood (the type species, Figs. 235-237) examined were determined by Berland. In abdominal shape this species is intermediate between what has been called *Ulesanis* by American arachnologists, and the spiny *Phoroncidia*. The genitalia are similar to those of *Ulesanis* and the two genera should be combined. Only details of genitalia separate the Japanese *Sudabe pilula* Karsch from the North American *Phoroncidia americana* (Emerton) (Fig. 244); otherwise the species could be confused. The genitalia and carapace shape of *Wibrada longiceps* Keyserling (Figs. 240-243) suggest that it is a *Phoroncidia*. *Heribertus rubromaculata* Keyserling is probably a *Phoroncidia;* the abdomen is flattened. Specimens placed in *Tricantha* differ only in shape of abdomen (Fig. 247).

Wirada Keyserling

Figures 248-250

Carapace with eye region projecting; clypeus fairly straight, sloping back toward base of chelicerae. Carapace and sternum tuberculate (Fig. 250). Chelicerae small with two teeth on anterior margin, none posterior (in *W. tovarensis* Simon). Legs short, leg IV slightly longer than I. Tarsi longer than metatarsi. Abdomen similar in both sexes, dorsoventrally flattened, covered completely with a circular sclerotized dorsal shield. A large shield surrounds pedicel and most of venter and a sclerotized

ring surrounds spinnerets. Colulus replaced by two setae, but sometimes difficult to see, hidden by sclerotized ring.

Epigynum heavily sclerotized with distinct openings. Two large seminal receptacles present. Palpus with paracymbial hook functional. The embolus continues proximally. The shape of this proximal extension might indicate that it is homologous with the median apophysis (Fig. 249). If this is true, the large triangular sclerite that fits into the paracymbial hook is the radix. It would be the only genus in which the radix fits against the paracymbial hook.

The carapace and sternum are tuberculate as in spiders of the genus *Crustulina;* however, *Wirada* differs in lacking the distal process on the palpal cymbium and in having two setae replacing the colulus. *Wirada* differs from *Dipoena* in having only two seminal receptacles; from *Phoroncidia* by having the carapace and sternum tuberculate, and by a different palpal structure. The relatively simple palpus and the long tarsi are as in the family Symphytognathidae. Perhaps, like many symphytognathids, *Wirada* lacks lungs. Lack of specimens prevented a detailed study. Unlike symphytognathids, *Wirada* lacks teeth on the posterior margin of the chelicerae.

Two South American species.

D. Theridiids with a large colulus.

THEONOE Simon

Figures 251-252

Carapace robust, high. Chelicerae with four anterior teeth. Legs short; leg IV longer than I; length of fourth patella-tibia half to equal carapace length. Tarsi longer than metatarsi. Abdomen oval. Colulus large. Very small, less than 1.5 mm total length.

Epigynum with openings indistinct. Palpus with median apophysis fused to embolus. Radix absent. Cymbium extends beyond alveolus (Fig. 251).

Separated from *Achaearanea* by large colulus and oval abdomen, from *Comaroma* and symphytognathids by structure of palpus (Fig. 251).

Only two very similar species known, one from Europe, the other from North America.

The long tarsi and the relatively simple palpus combined with a large colulus indicate relationship of this genus to *Mysmena* and other symphytognathids.

Latrodectus Walckenaer

Figures 14, 15, 253, 254

Carapace rather wide in thoracic region. Lateral eyes separated. Chelicerae without teeth (Figs. 14, 15). First patella-tibia 1.5 to 2.2 times carapace length. Abdomen globular. Colulus large. Bite poisonous to some vertebrates.

Epigynum sclerotized, with ovoid depression. Two dumbbell-shaped seminal receptacles (Fig. 254) and coiled connecting ducts (Fig. 253). Palpus with irregularly shaped cymbium, long coiled embolus, sclerotized radix, median apophysis and small conductor.

Separated from most genera by large colulus; from *Steatoda* by toothless chelicerae and by dumbbell-shaped seminal receptacles.

Six very similar species.

Cosmopolitan, absent from colder portions of Eurasia.

Steatoda Sundevall

Figures 255-271

Carapace as in *Theridion*, but relatively narrow in eye region and more heavily sclerotized (Fig. 260). Male with stridulating ridges posterior on each side. Lateral eyes sometimes separated. Chelicerae sometimes enlarged in male, with one or two teeth on anterior margin, none posterior in females. Leg I or IV longest; longest patella-tibia 0.8 to 2 times carapace length. Abdomen suboval, male with more or less sclerotized ring around pedicel with stridulating structures. Usually abdomen reddish brown to purplish black, often with a white line around anterior margin (Figs. 259, 260). Colulus large.

Two seminal receptacles present and usually a pair of thin-walled sacs (Fig. 269). Palpus with all sclerites, usually a large radix (Fig. 258), paracymbial hook in back of cymbium, not on margin.

The separation of this genus from *Enoplognatha* is probably arbitrary. Separated from females of *Enoplognatha* by lacking tooth on posterior margin of chelicerae; from males by having paracymbial hook in back of cymbium, not on outside margin; or if the hook is on outside margin, chelicerae are not enlarged. *Steatoda* is not close to *Dipoena*. The large colulus, structure of the chelicerae, two seminal receptacles, structure of the palpus of *Steatoda* removes it from *Dipoena*, even though some species

of both genera (as well as of other genera) may have the anterior median eyes largest.

Cosmopolitan.

As a result of defining the genus on eye position, a character variable even within individual species (Levi, "1959" [1960]), there are numerous synonyms for *Steatoda,* genera based on type species having the eyes slightly different in size or position.

Ancococlus livens Simon (Figs. 266-268) differs from other species only in that the median apophysis and paracymbial hook do not touch. The eye region is relatively narrow. *Ancococlus* is the most distinct of the genera synonymized with *Steatoda.* No characters are known that separate *Stethopoma cingulatum* Thorell (Figs. 264, 265), *Steassa marmorata* Simon (Fig. 263), and *Argyroelus micans* Hogg (Figs. 269, 271) from *Steatoda. Asagenella erigoniformis* (O.P.-Cambridge) (Figs. 261, 262) is a *Steatoda;* it has been known in America by the name *S. septemmaculata* (Keyserling) [= *Lithyphantes septemmaculata* Keyserling].

Crustulina Menge

Figures 272-274

Carapace, sternum covered with tubercles (Fig. 272). No teeth on posterior margin of chelicerae. Leg I or IV longest. Longest patella-tibia slightly longer or shorter than carapace length. Abdomen with sclerotized ring around pedicel in both sexes. Colulus large. Brownish coloration.

Epigynum with a raised transverse bridge. Palpal cymbium with median distal process (Figs. 273, 274). Embolus complicated, with a large hook; radix and median apophysis present (Fig. 274).

Separated from *Robertus* and *Enoplognatha* by lack of teeth on the posterior margin of chelicerae; from *Steatoda* by tubercles on carapace; from all three by distal process of palpal cymbium.

Several similar species.

Known from Europe and North America; some species have been described from Africa.

Craspedisia Simon

Figures 275-280

Carapace of female as in *Steatoda,* that of male with a projection on clypeus (Fig. 276). Chelicerae with a tooth on anterior

margin. Abdomen oval, with (broken) sclerotized ring around pedicel in both sexes (Fig. 275). Some sclerotized spots on venter. Colulus large.

Epigynum with a raised transverse bridge as in allied genera. Palpus with all sclerites; paracymbial hook on rim of cymbium, and a large complex embolus (Fig. 280).

Male separated from *Crustulina* and *Steatoda* by clypeal projection; female separated from *Crustulina* by smoother carapace, from *Steatoda* by sclerotized ring around pedicel.

Only two species known, from tropical America.

Enoplognatha Pavesi

Figures 20, 21, 281-285

Carapace as in *Steatoda,* not modified. Chelicerae of male enlarged (Fig. 281), chelicerae of female with several teeth on anterior margin, one tooth posterior(Figs. 20, 21). First or fourth leg longest. Longest patella-tibia 1 to 1.8 times carapace length. Abdomen suboval. Abdomen of male with a carina above pedicel, sometimes dorsum sclerotized. Colulus large. Usually dark colored, with a dorsal pattern on abdomen; white pigment, if present, in minute spots.

Epigynum heavily sclerotized. Palpus with all sclerites, paracymbium on margin of cymbium, and a prominent radix supporting embolus (Fig. 282).

Females separated from *Robertus* and *Steatoda* by having one tooth on posterior margin of chelicerae, males by structure of palpus. It is believed that there are species intermediate between *Steatoda* and *Enoplognatha.*

Cosmopolitan.

Symopagia orcophila Simon (Figs. 283-285) is an *Enoplognatha;* it has a tooth on posterior margin of the chelicerae; the carapace is highest in the thoracic region.

Icona Forster

Figures 286-289

Carapace as in *Steatoda,* not modified but less sclerotized. Chelicerae straight with two teeth on anterior margin, one posterior. Legs of medium length. Abdomen suboval. Colulus large. Light colored.

Female epigynum with openings leading into two atria, these into the seminal receptacles (Figs. 287, 288). Male palpus with

a large conductor, large embolus, and large radix; median apophysis very small, not functional in holding bulb against cymbium; paracymbial hook near margin. Cymbium suboval in outline (Figs. 286, 289).

Separated from *Enoplognatha* by different structure of palpus, and by being very lightly sclerotized.

One species, from New Zealand.

Robertus O.P.-Cambridge

Figures 290, 291

Carapace sclerotized, rounded in front, rather high; clypeus rounded. Chelicerae strong, with three large anterior teeth and two posterior denticles or teeth. Legs relatively short and strong; first subequal to fourth. First patella-tibia equal to carapace length or slightly shorter. Abdomen oval. Colulus large. Abdomen uniformly colored without pattern.

Palpus with all sclerites present, but reduced, and relatively simple in shape (probably secondarily) (Figs. 290, 291). Cymbium widest at proximal end, tapering to a relatively narrow tip. Paracymbial hook on margin (Fig. 291).

Separated from *Comaroma* by having eight eyes or anterior medians subequal to the others and from *Enoplognatha* by having several denticles on the posterior cheliceral margin, by not having male chelicerae enlarged, and by lacking a pattern on the dorsum of the abdomen.

Probably only Europe and North America.

Comaroma Bertkau

Figures 292-294

Carapace as in *Steatoda,* but heavily sclerotized. Six eyes, or if eight, then diameter of anterior medians less than radius of posterior eyes. Chelicerae strong with three anterior teeth and posterior denticles. First and fourth legs subequal. First patella-tibia slightly shorter than carapace. Tarsus slightly longer than metatarsus. Abdomen very heavily sclerotized. Large colulus. Small size, less than 1.5 mm total length.

Epigynum with openings indistinct. Palpus with paracymbium on rim of cymbium, median apophysis reduced in size and not functional in holding bulb against cymbium; embolus of complex shape (Fig. 294).

Separated from *Phoroncidia* and *Pholcomma* by large colulus, from *Robertus* by heavy sclerotization of abdomen and reduced anterior median eyes. This genus may be close to Symphytognathidae.

Two species known from southeastern Europe, one from California and one or two from Japan.

Archerius mendocino Levi (from California) differs from *Comaroma simoni* Bertkau (found in Europe) in being smaller and in details of the genitalia.

Synotaxus Simon

Figures 295-298

Carapace slightly flattened, eyes overhanging clypeus. Chelicerae small, probably with one or two teeth on the anterior margin, none posterior. Legs very long, first femur 1.5 times length of body. Abdomen with a long extension beyond spinnerets (Fig. 295). Colulus large. Uniformly white in color.

Palpus with paracymbium absent; median apophysis very small; conductor may be absent. Haematodocha may attach bulb to dorsum of alveolus of cymbium rather than to proximal end. Palpal patella of male has a spur (Fig. 298).

Separated from *Argyrodes* by palpal patellar spur, and by unmodified eye region of male.

Only four species known, from South America.

Argyrodes Simon

Figures 6, 299-305

Carapace of male with eye and clypeal region usually swollen, projecting, or with a seam below eyes (Figs. 299, 301). Chelicerae with one to several teeth on anterior margin, one, and sometimes denticles, on posterior margin. Legs sometimes long, first longest. Comb often absent or reduced to a few setae. Fourth tarsal claws shifted and facing retro-laterally (or comb possibly prolateral). Middle tarsal claw longer than laterals (Fig. 6). Abdomen sometimes higher than long, but usually extending beyond spinnerets, filiform or often with tubercles on posterior end (Figs. 303-305). Large colulus usually with only two setae.

Palpus with all sclerites present (Fig. 302).

Warm parts of the world, commensals in webs of other spiders.

The shape of the eye region of males and the unusual shape of the abdomen separate this genus from others having a colulus.

Faiditus ecaudatus Keyserling is an *Argyrodes* (*F. bruncoviridis* Mello-Leitão belongs in *Episinus*). In a revision of American species of *Argyrodes, Rhomphaea* and *Ariamnes* (Exline and Levi, 1962), it has not been possible to find characters that keep these genera apart. *Argyrodes elevatus* Taczanowski and *A. bonadea* (Karsch) are similar to the type species, illustrated in the revision of American species.

Genera Transferred to Other Families

Characters of families related to Theridiidae are discussed above and need not be repeated here.

No specimens of *Dubiaranea argentcovittata* Mello-Leitão were available for study. It is believed to be a Linyphiidae, although its placement remains uncertain. *Sedasta ferox* Simon (Fig. 306) was described from juveniles and though the correct placement is uncertain, it is not a theridiid. The colulus is replaced by two setae; the posterior cheliceral margin has a dentiele, the anterior margin is bare. The chelicerae are very large. The abdomen is slightly pointed behind. *Perania pallida* Thorell (Fig. 307), described from a juvenile female, has a small colulus with two setae, only six eyes, and a keel on each of the chelicerae. No other theridiids are known to have a long cheliceral keel. The abdomen is soft, the legs of medium length, as in *Theridion*. There is a very slightly sclerotized ring around the spinnerets. *Phaedima granulosa* Thorell (Fig. 308) is very similar to *Perania pallida;* it is very heavily selerotized, total length 6 mm; the chelicerae are as in *Perania* and there are only six eyes. It is likely that *Perania pallida* is a juvenile female of *Phaedima granulosa* Thorell. Both come from Sumatra. They are probably Tetrablemmidae.

Most members of the family Symphytognathidae were formerly placed with the theridiids. Most are small species. The following species, all types of genera, have to be transferred to Symphytognathidae: *Mysmena leucoplagiata* (Simon), *Cepheia longiseta* Simon (Figs. 309, 310), *Synaphris letourneuxi* Simon (Fig. 311), *Tamasesia rotunda* Marples, *Taphiassa impressa* Simon (Figs. 312, 313), *Troglonota granulum* Simon (Figs. 314-316), *Zangherella minima* Caporiacco (Figs. 317-320), the six eyed *Epecthina circinata* Simon (Figs. 321-323) and *Mysmenopsis femoralis* Simon. The last species has been illustrated by

W. J. Gertsch (1960) from our sketches. Lack of knowledge of generic characters in the family prevented detailed description at the time we examined the specimens. The very small size of the specimens and the paucity of material made it impossible to make detailed sketches of the palpi.

The type of *Artonis* Simon, *Anania biturberculata* Thorell (Fig. 324), is an argiopid. The abdomen resembles that of *Chrysso* or *Argyrodes;* it is longer than wide or high and has a pair of tubercles at the posterior dorsal tip. The chelicerae have many teeth like those of Argiopidae. Specimens of *Chorizoopes frontalis* O.P.-Cambridge are located in the Paris museum; these specimens, determined by Simon, may not be the types. They are argiopids having a large colulus; the anterior margin of each chelicera has a row of large denticles, becoming long teeth at the proximal end. The argiopid-like palpus has the paracymbial hook at the base of the cymbium. *Paurotylus depressus* Tullgren was recognized by Tullgren as an argiopid. Petrunkevitch (1928) erroneously placed *Paurotylus* into the Theridiidae. Unfortunately he has been followed by others who, like Petrunkevitch, presumably have not examined the specimens.

Mecynidis dentipalpis Simon (Figs. 325-327) is probably a linyphiid but may be an argiopid. The paracymbium (P in Fig. 327) seems to be a separate sclerite, although this is not certain. The carapace is wide anteriorly as in some argiopids. The palpal femur has a row of thorns. Two-thirds of the dorsum of the abdomen is covered by a scutum. The chelicerae have two very large teeth on the anterior margin, and only two on the posterior. The types of *Liger incompta* O.P.-Cambridge were thought to be lost and another specimen accidentally introduced into the vial. However, Cambridge's poor illustrations seem to have been made from the specimen in the vial, a typical linyphiid (Figs. 328, 329). We compared the description and original illustration with the specimen and believe it is the type.

Theridilella zygops Chamberlin and Ivie, known only from an immature female, is a theridiosomatid, probably of the genus *Theridiosoma.* Specimens examined of *Spheropistha melanosoma* Yaginuma, also described from the female only, at first seemed puzzling. It resembled a *Dipoena* but had a large colulus. It is believed now to belong to the theridiosomatids, although this can be made certain only by finding a male. We agree with the late Miss Bryant, who illustrated the species, that *Tekella absidata* Urquhart, is probably a theridiosomatid, possibly an argiopid.

Enthorodea atricolor Simon (Figs. 330-332), also known from the female only, is believed to be a *Theridiosoma.*

R. R. Forster (*in litt.*) suggested that the genus *Nicodamus* (Figs. 333, 334) belongs to the family Zodariidae.

Relationships

The Theridiidae are generally considered more primitive than the related families Linyphiidae and Argiopidae. Evidence comes not only from the increased structural complexity of genitalia in the latter two families, but also from their behavior. Theridiids build irregular webs, while the orb-webs of argiopids and the sheet-webs of linyphiids may be considered evolutionary refinements. The simple palpus of Symphytognathidae is probably a secondary simplification, as evidenced by vestiges of sclerites, and by the orb-webs built by some species.

The relationship of different theridiid genera to each other is puzzling. The Theridiidae can not be split into subfamilies, with one possible exception. *Dipoena* and *Euryopis* (and perhaps *Audifia*) might represent a separate line of evolution, judging by the presence of four seminal receptacles rather than two, by the tendency of the palpal duct to be tortuous and travel through the length of the median apophysis (also found in some other theridiids), by the relatively large eye area, and by the long flat fang of the chelicerae (Figs. 9, 10), probably for catching ants. However, these two genera are not distinct and often careful examination is necessary for correct generic placement. Other genera have a tendency to auxillary lobes in the connecting ducts (i.e., *Pholcomma*). Some species of *Euryopis* have only two seminal receptacles. The fact that these species have a relatively simple palpus resembling that of *Achaearanea* may be of significance in postulating the origin of the group. Another genus, *Theridula,* has a genitalic plan that is quite different and might also represent a separate evolutionary line. Allied to *Theridula* might be *Paratheridula.* The latter genus, however, has more generalized genitalia and, as its former inclusion in the genus *Theridion* indicates, few other differences. While other genera fall into groups, for instance: *Steatoda-Latrodectus-Crustulina-Enoplognatha; Episinus-Spintharus-Thwaitesia; Chrysso-Coleosoma-Theridion-Thymoites,* there is no evidence that they are sufficiently distinct to be considered subfamilies. For separating genera, considerable weight is given to the size of the colulus. The phylogenetic value of this structure should, however,

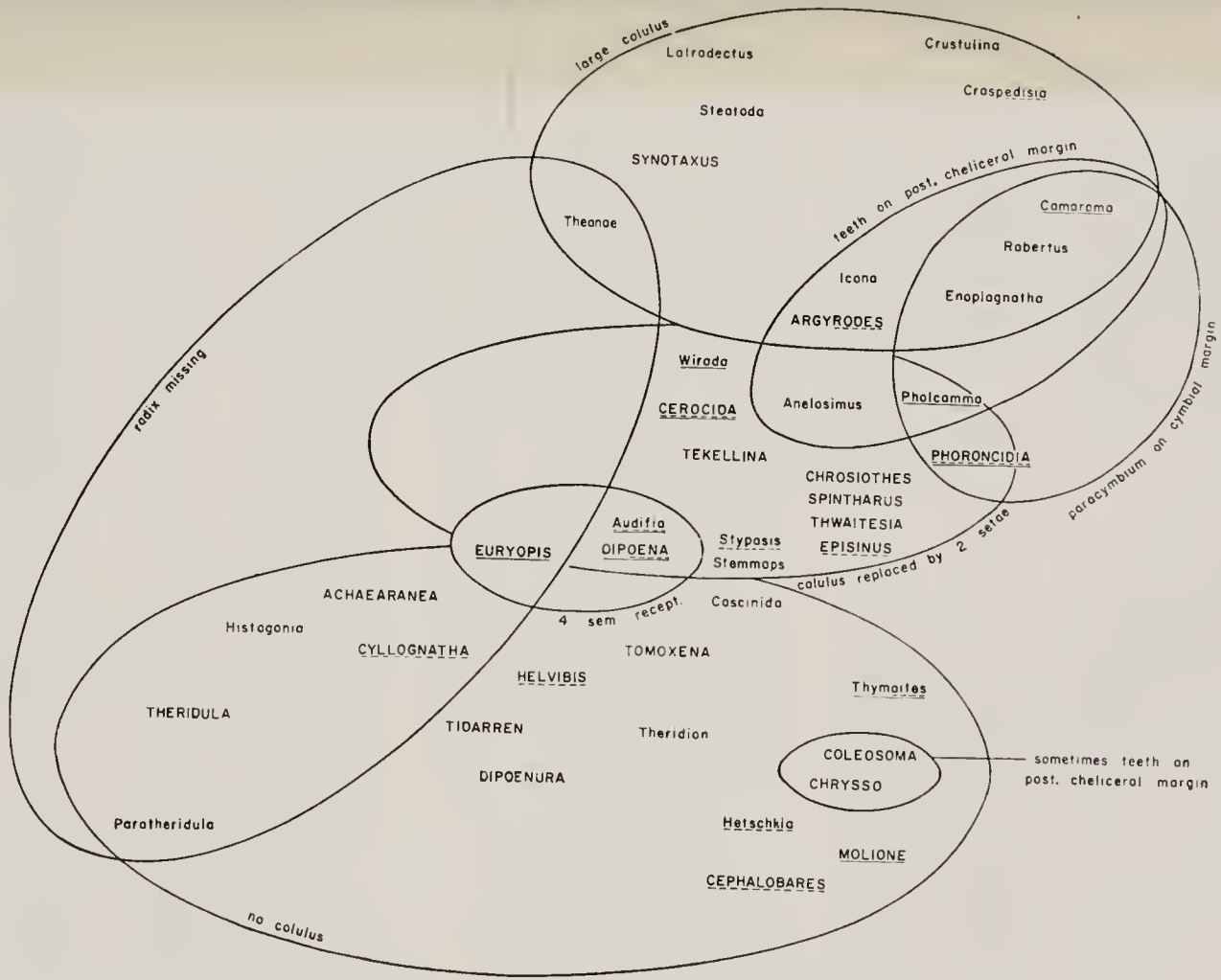

TABLE 2.

Theridiid genera. Circles represent characters believed to be of phylogenetic importance. Genera printed in lower case have abdomen generally spherical to longer than wide and high. Genera printed in upper case have abdomen generally modified higher than long, with humps, wider than long, or extended beyond spinnerets. Underlined genera may have the abdomen heavily sclerotized with scutes, and sclerotized ring around spinnerets. A dotted line indicates that the carapace shape may be modified, half a dotted line indicates modification in the male only. Such a modified carapace may be stalked, ovoid, have the eye region projecting or may have horns, projections in clypeal or eye region.

not be over-rated. Some *Euryopis* lack a colulus, others have two setae in its place. The only difference between *Coscinida* and *Stemmops* is that the former lacks a colulus, while in *Stemmops* it is replaced by two setae. Thus the two might still be considered one genus. On the other hand, the few genera having a large colulus are probably closely related, judging by the genitalia, and are probably more distinct from others. This latter group is closest in genitalic structure to the family Argiopidae. Some of the group criteria used by Simon have no phylogenetic significance by modern standards, and would obscure natural groups of genera. For instance, Simon considered the large anterior median eyes of some *Steatoda* and some *Dipoena* to be sufficiently important to relate these otherwise very different genera. And Simon's criterion of heavy sclerotization would have combined the otherwise very different genera *Thymoites*, *Phoroncidia*, and *Comaroma*.

It is believed that structures like the radix and median apophysis may have evolved several times (Levi, 1961).

The diagram (Table 2) attempts to organize characters and genera. No attempt was made to connect the genera by a phylogenetic tree. The genera on the lower left have the simplest and probably most primitive genitalia, and those on top are the most complex and probably most advanced.

BIBLIOGRAPHY

Chickering, A. M.

1943. Twenty-one new species of *Dipoena* (Theridiidae) from Panama. Trans. Amer. Micros. Soc., vol. 62, pp. 329-378.

1948. Four new species of *Dipoena* (Araneae: Theridiidae) from Panama. *Ibid.*, vol. 67, pp. 331-340.

Exline, H. and H. W. Levi

1962. American spiders of the genus *Argyrodes*. Bull. Mus. Comp. Zool., vol. 127, no. 2 (in press).

Gertsch, W. J.

1960. Descriptions of American spiders of the family Symphytognathidae. Amer. Mus. Novitates, no. 1981, pp. 1-40.

Hennig, W.

1950. Grundzüge einer Theorie der phylogenetischen Systematik, Deutscher Zentralverlag, Berlin, pp. 370.

Kaston, B. J.

1946. North American spiders of the genus *Ctenium*. Amer. Mus. Novitates, no. 1306, pp. 1-19.

LEVI, H. W.

1953. New and rare *Dipoena* from Mexico and Central America (Araneae: Theridiidae). Amer. Mus. Novitates, no. 1639, pp. 1-11.

1953. Spiders of the genus *Dipoena* from America North of Mexico (Araneae: Theridiidae). *Ibid.*, no. 1647, pp. 1-39.

1954. Spiders of the new genus *Theridiotis* (Araneae: Theridiidae). Trans. Amer. Micros. Soc., vol. 73, no. 2, pp. 177-189.

1954. Spiders of the genus *Euryopis* from North and Central America (Araneae: Theridiidae). Amer. Mus. Novitates, no. 1666, pp. 1-48.

1954. The spider genus *Theridula* from North America, Central America, and the West Indies (Araneae: Theridiidae). Trans. Amer. Micros. Soc., vol. 73, no. 4, pp. 331-343.

1955. The spider genera *Coressa* and *Achacaranea* in America North of Mexico (Araneae: Theridiidae). Amer. Mus. Novitates, no. 1718, pp. 1-33.

"1954" [1955]. The spider genera *Episinus* and *Spintharus* from North America, Central America, and the West Indies (Araneae: Theridiidae). Jour. New York Ent. Soc., vol. 62, pp. 65-90.

1955. The spider genera *Oronota* and *Stemmops* in North America, Central America and the West Indies (Araneae: Theridiidae). Ann. Ent. Soc. Amer., vol. 48, pp. 333-342.

1957. The spider genera *Enoplognatha, Theridion* and *Paidisca* in America north of Mexico (Araneae: Theridiidae). Bull. Amer. Mus. Nat. Hist., vol. 112, no. 1, pp. 1-123.

"1956" [1957]. The spider genera *Neottiura* and *Anclosimus* in America (Araneae: Theridiidae). Trans. Amer. Micros. Soc., vol. 75, no. 4, pp. 407-421.

"1955" [1957]. The spider genera *Tidarren* and *Chrysso* (Araneae: Theridiidae). Jour. New York Ent. Soc., vol. 63, pp. 59-81.

1957. The North American spider genera *Paratheridula, Tekellina, Pholcomma* and *Archerius* (Araneae: Theridiidae). Trans. Amer. Micros. Soc., vol. 74, no. 2, pp. 105-115.

1957. The spider genera *Crustulina* and *Steatoda* in North America, Central America, and the West Indies (Araneae: Theridiidae). Bull. Mus. Comp. Zool., vol. 117, no. 3, pp. 367-424.

"1957" [1958]. Spiders of the new genus *Arctachaea* (Araneae: Theridiidae). Psyche, vol. 64, pp. 102-106.

1959. The spider genus *Latrodectus* (Araneae: Theridiidae). Trans. Amer. Micros. Soc., vol. 78, pp. 7-43.

1959. The spider genus *Coleosoma* (Araneae: Theridiidae). Breviora, no. 110, pp. 1-11.

1959. The spider genera *Achaearanea, Theridion,* and *Sphyrotinus* from Mexico, Central America and the West Indies (Araneae: Theridiidae). Bull. Mus. Comp. Zool., vol. 121, pp. 57-163.

"1959" Problems in the spider genus *Steatoda* (Theridiidae). Syst. [1960a]. Zool., vol. 8, no. 3, pp. 107-116.

"1959" The spider genus *Styposis* (Araneae: Theridiidae). Psyche, vol. [1960b]. 66, pp. 13-19.

1961. Evolutionary trends in the development of palpal sclerites in the spider family Theridiidae. Jour. Morph., vol. 108, pp. 1-10.

Locket, G. H., and A. F. Millidge

1953. British spiders. The Ray Soc., vol. 2, pp. 37-91.

Mayr, E.

1942. Systematics and the origin of species. Columbia Univ. Press, New York.

Mayr, E., E. C. Linsley, and R. L. Usinger

1953. Methods and principles of systematic zoology. McGraw-Hill Book Co., New York.

Nielsen, E.

1931. The biology of spiders. Levin and Munksgaard, Copenhagen, vol. 1, pp. 188-202; vol. 2, pp. 521-585.

Petrunkevitch, A.

1928. Systema Araneorum. Trans. Connecticut Acad. Sci., vol. 29, pp. 1-270.

Simpson, G. G.

1961. Principles of animal taxonomy. Columbia Univ. Press, New York.

Tullgren, A.

1949. Bidrag till kännedomen om den svenska spindelfaunen III. Ent. Tidskr., vol. 70, pp. 33-64.

Wiehle, H.

1931. Neue Beiträge zur Kenntnis des Fanggewebes der Spinnen aus den Familien Argiopidae, Uloboridae und Theridiidae. Zeitschr. wiss. Biol., Abt. A, Morph. Ökol., vol. 22, pp. 349-400.

1937. Theridiidae oder Haubennetzspinnen. *in* Die Tierwelt Deutschlands, pt. 33, pp. 119-222.

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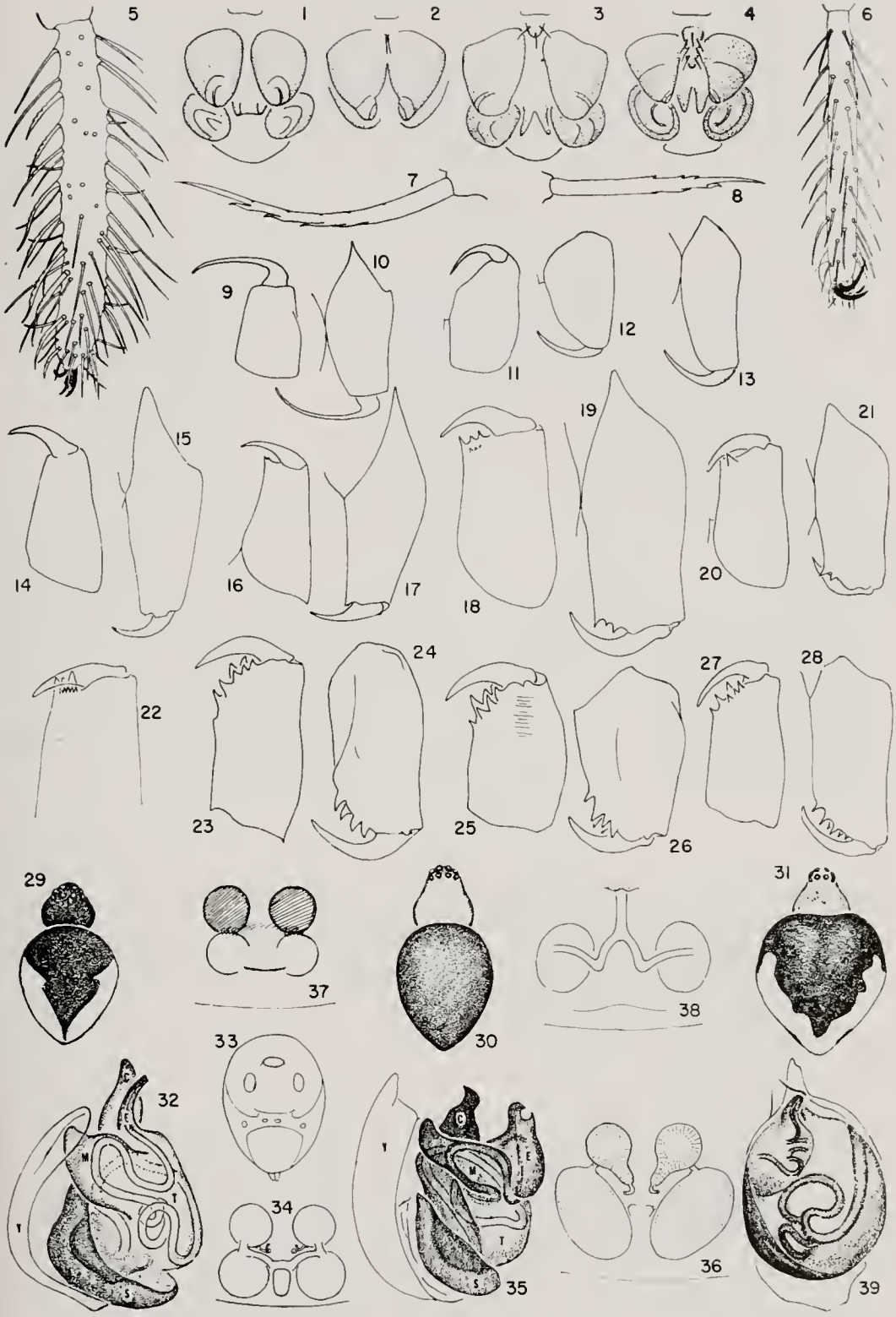
Abbreviations. C, conductor; E, embolus; M, median apophysis; S, subtegulum; T, tegulum; Y, cymbium.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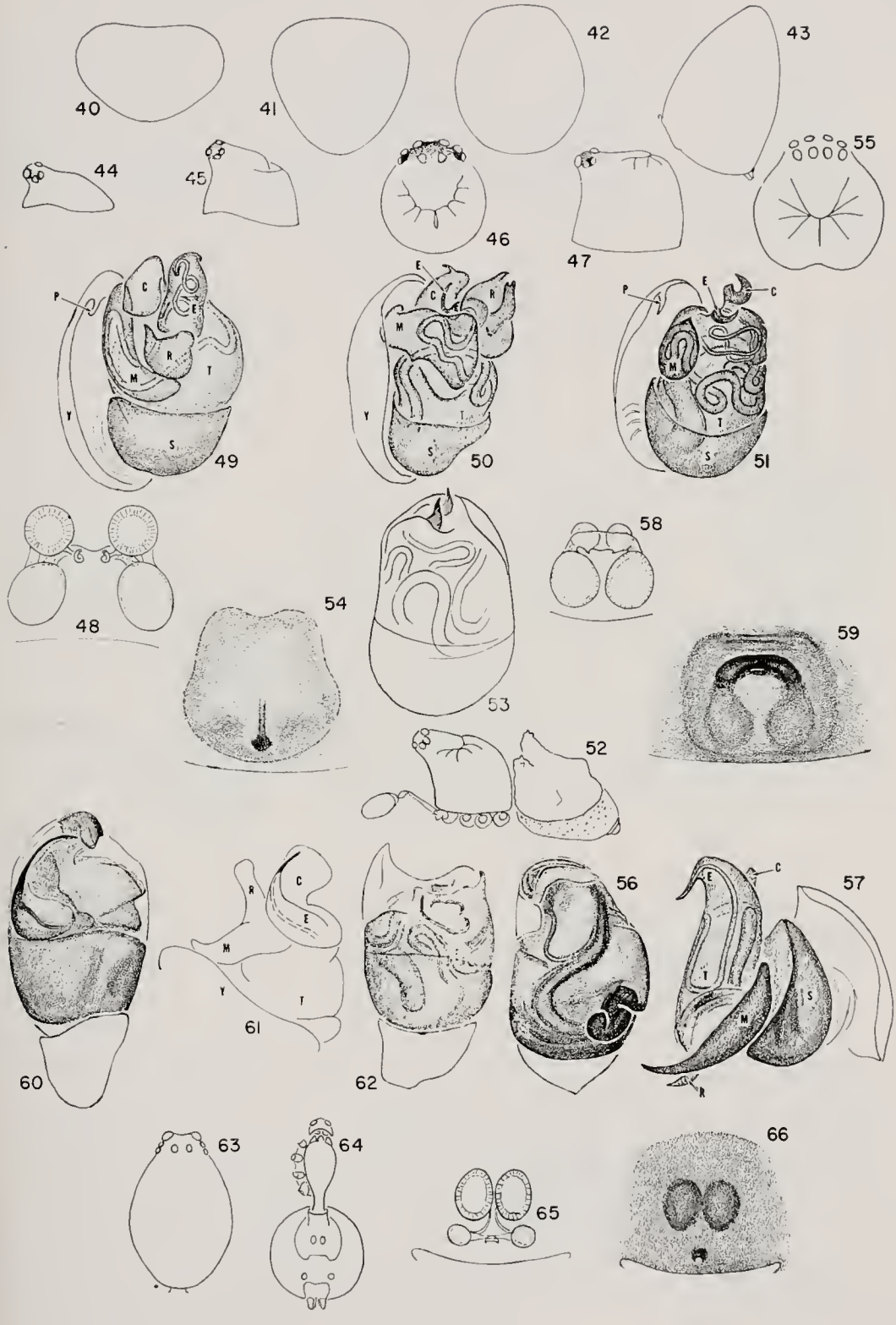
Abbreviations. C, conductor; E, embolus; M, median apophysis; P, paracymbium; R, radix; S, subtegulum; T, tegulum; Y, cymbium.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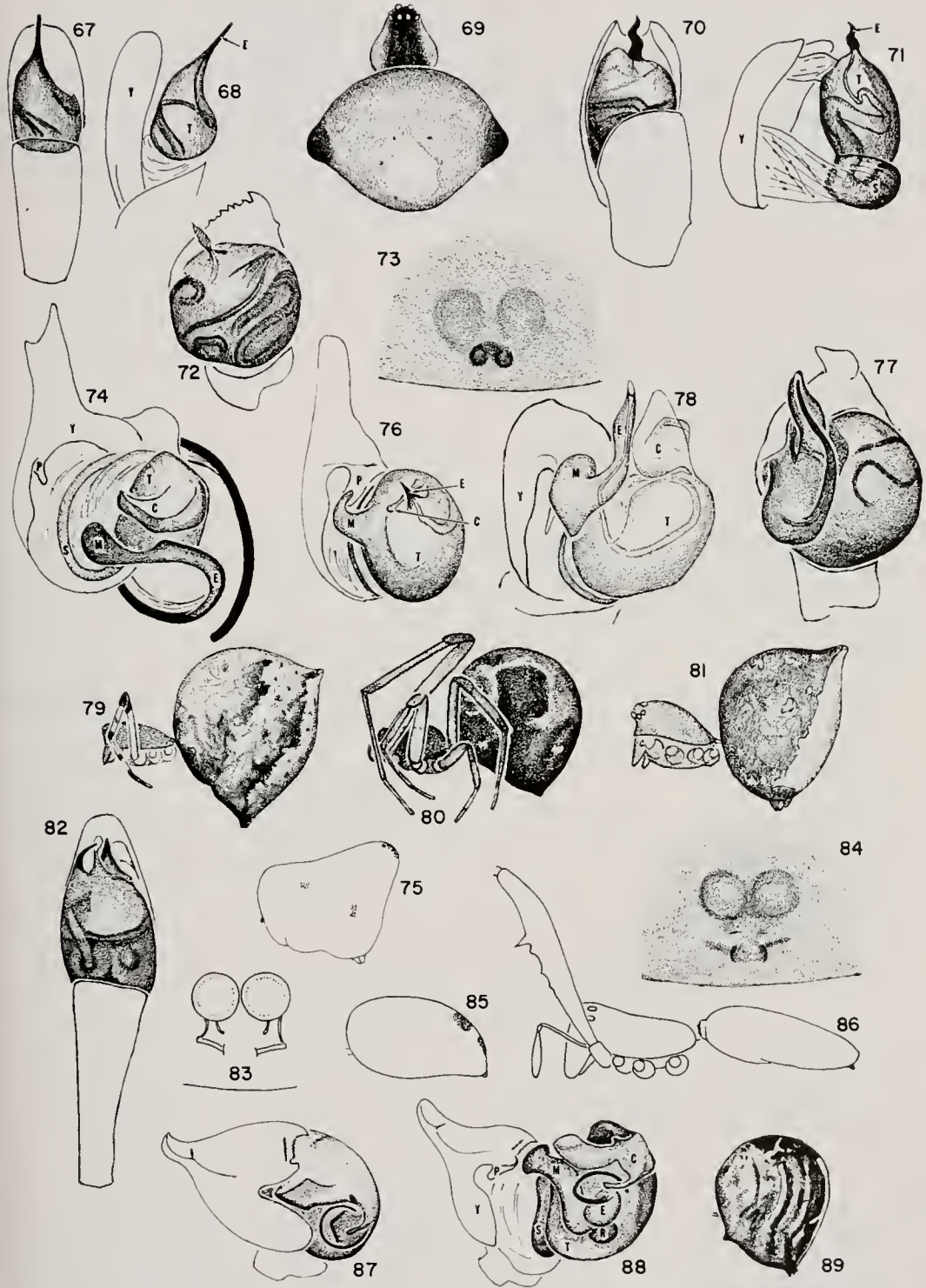
Abbreviations. C, conductor; E, embolus; M, median apophysis; P, paracymbium; R, radix; S, subtegulum; T, tegulum; Y, cymbium.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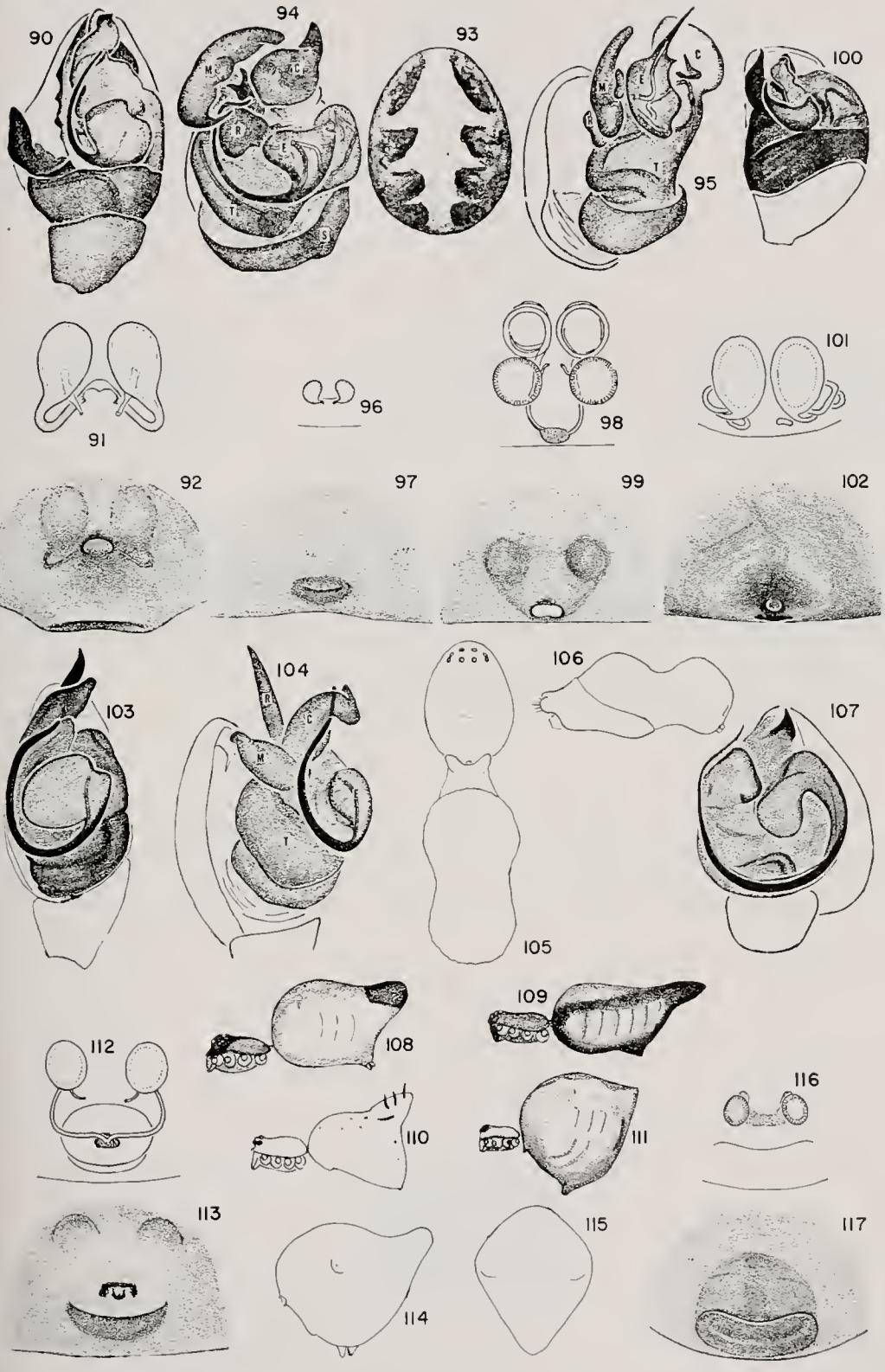
Abbreviations. C, conductor; E, embolus; M, median apophysis; R, radix; S, subtegulum; T, tegulum.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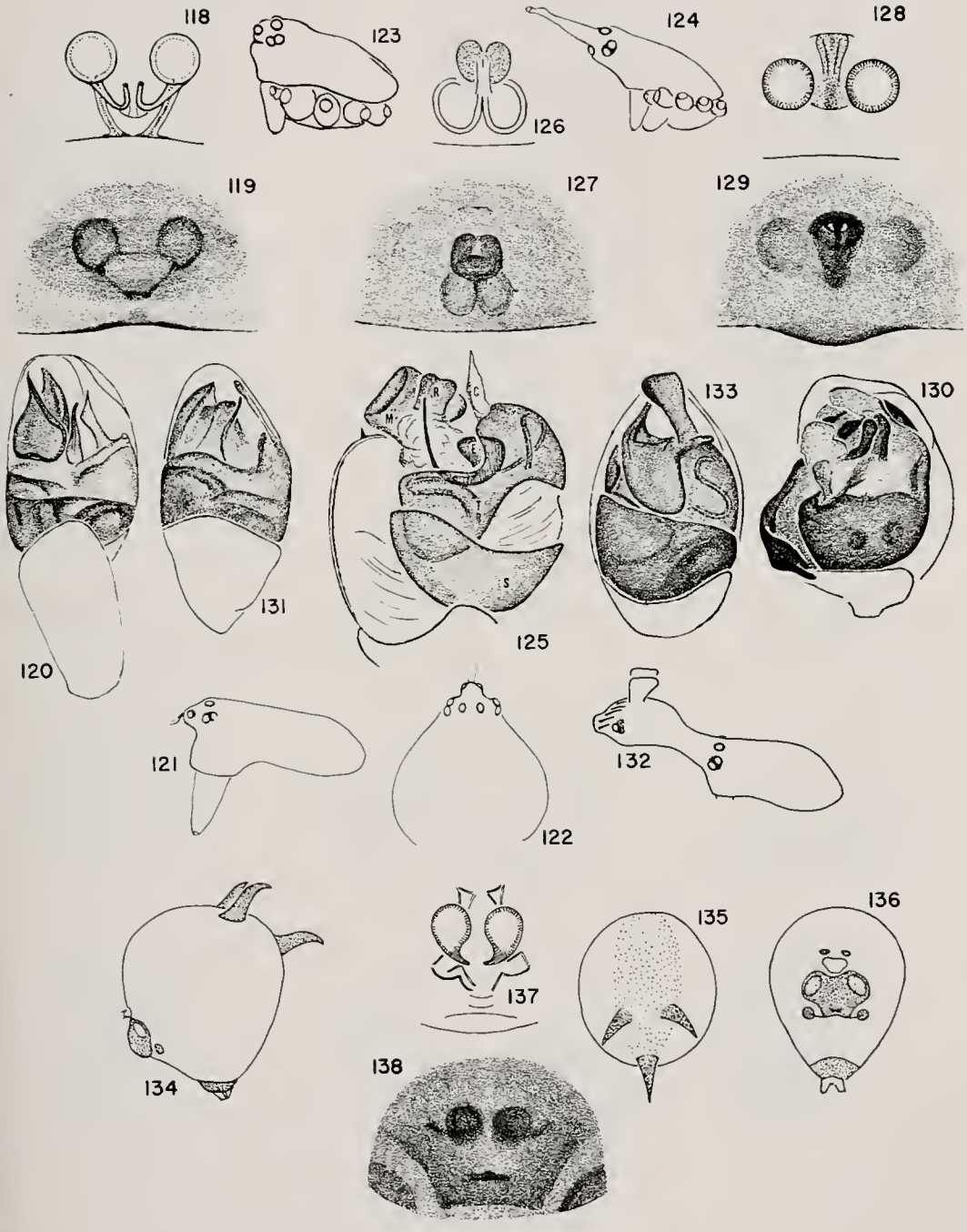
Abbreviations. C, conductor; E, embolus; M, median apophysis; R, radix; S, subtegulum; T. tegulum.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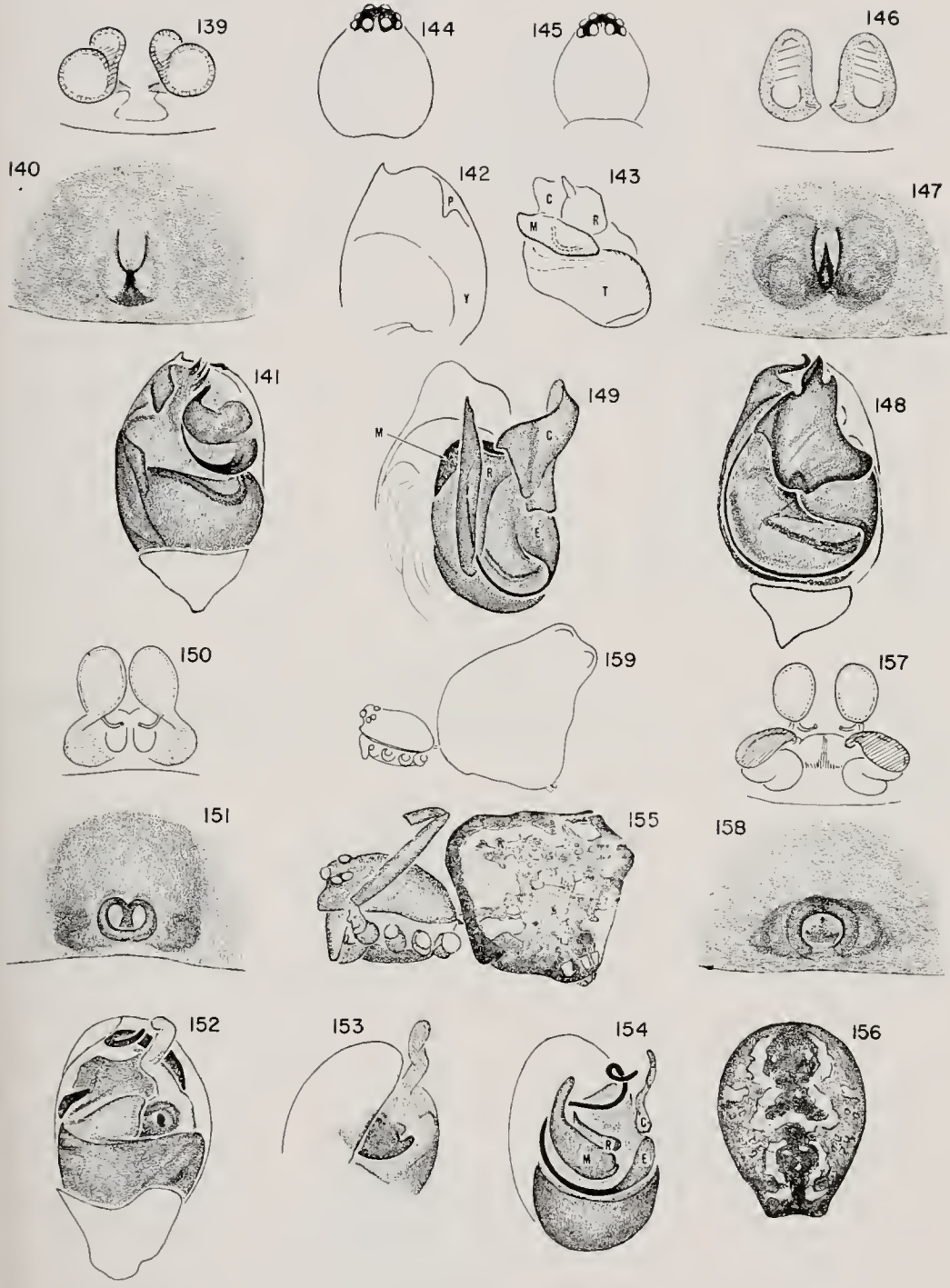
Abbreviations. C, conductor; E, embolus; M, median apophysis; P, paracymbium; R, radix; T, tegulum; Y, cymbium.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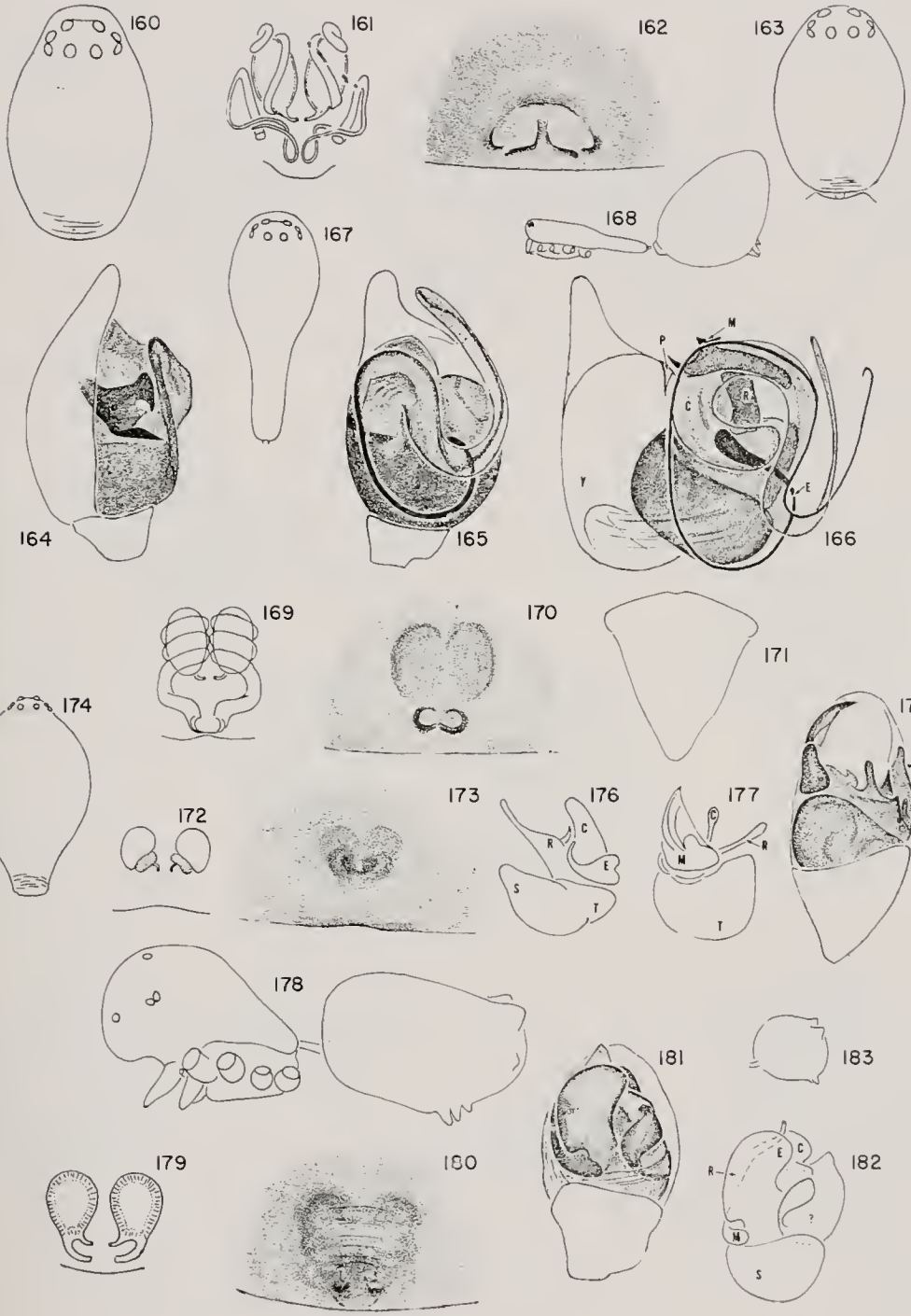
Abbreviations. C, conductor; E, embolus; M, median apophysis; P, paracymbium; R, radix; S, subtegulum; T, tegulum; Y, cymbium.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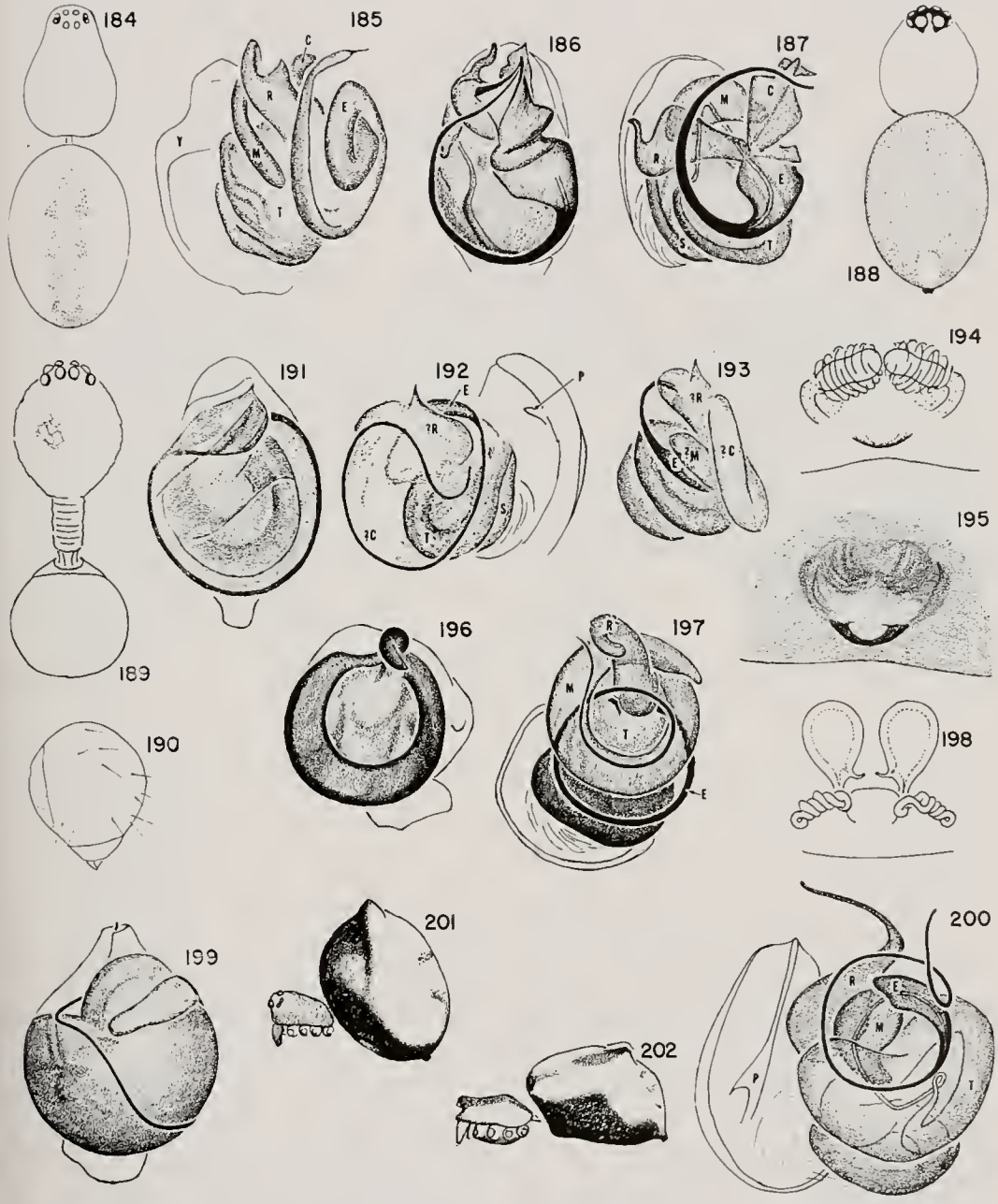
Abbreviations. C, conductor; E, embolus; M, median apophysis; P, paracymbium R, radix; S, subtegulum; T, tegulum; Y, cymbium.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Figs. 207-210. *T. margaritifera* O.P.-Cambridge. 207. Female abdomen, lateral view. 208. Epigynum cleared. 209. Epigynum. 210. Palpus.

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Episinus Latreille

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Fig. 221. *E. dominicus* Levi, female.

Figs. 222-223. *Ploeamis theridioides* Simon. 222. Female genitalia, dorsal view. 223. Epigynum.

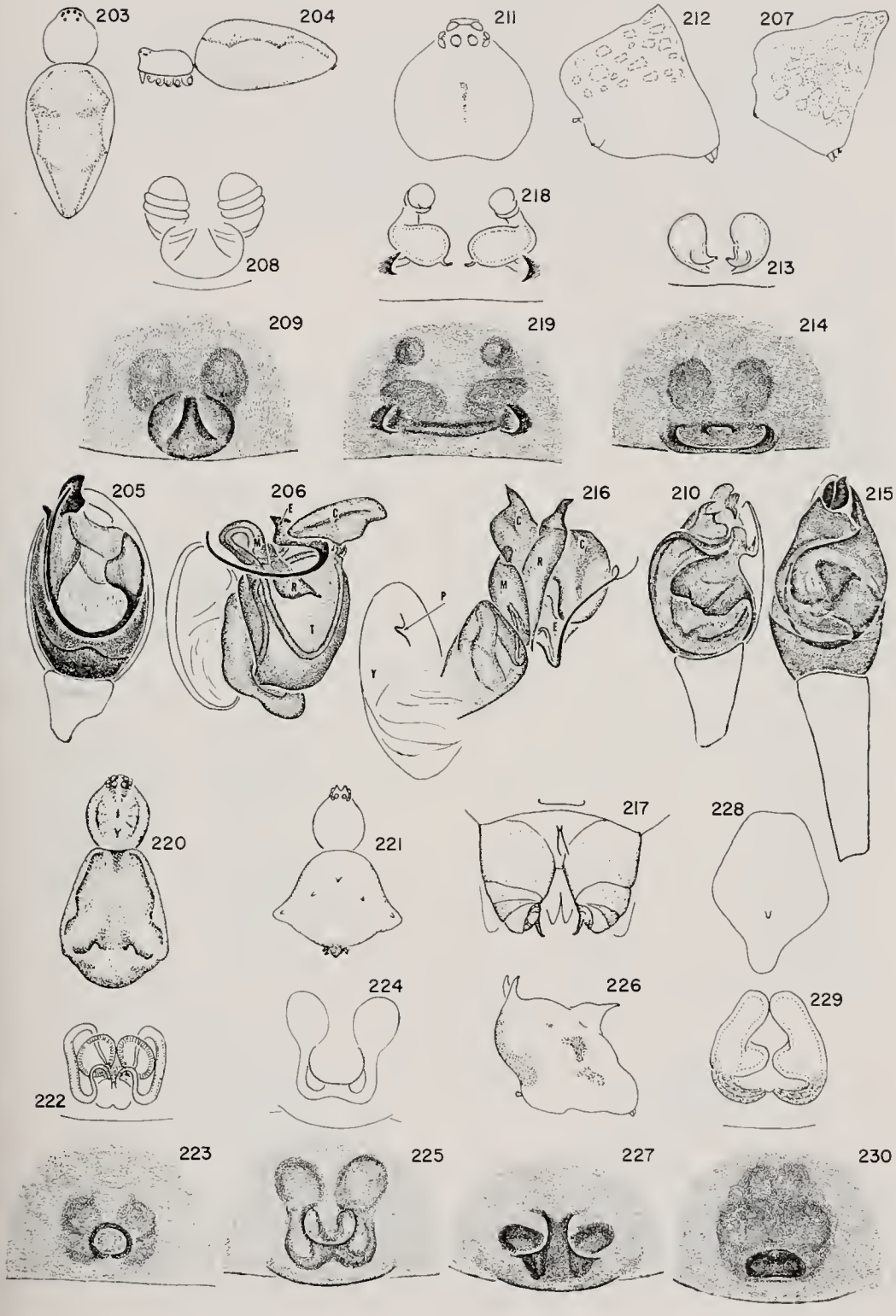
Figs. 224-225. *Hyptimorpha mirabilis* Strand. 224. Epigynum, cleared. 225. Epigynum.

Fig. 226. *Hyocrea implexa* Simon, juvenile abdomen, lateral view.

Fig. 227. *Episinopsis rhomboidalis* Simon, epigynum.

Figs. 228-230. *Moneta spinigera* O.P.-Cambridge. 228. Female abdomen, dorsal view. 229. Female genitalia, dorsal view. 230. Epigynum.

Abbreviations. C, conductor; E, embolus; M, median apophysis; P, paracymbium; R, radix; T, tegulum; Y, cymbium.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Styposis Simon

Figs. 231-233. *S. flavescens* Simon. 231. Female carapace. 232. Left palpus. 233. Palpal bulb, expanded, ectal view.

Pholcomma Thorell

Fig. 234. *P. hirsuta* Emerton, palpus expanded, ectal view.

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Fig. 235-237. *P. aculeata* Westwood (specimens determined by Berland). 235. Female. 236. Epigynum. 237. Palpus.

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Figs. 248-250. *W. punctata* Keyserling. 248. Palpus. 249. Palpus, cleared. 250. Male.

Abbreviations. C, conductor; E, embolus; M, median apophysis; P, paracymbium; R, radix; S, subtegulum; T, tegulum; Y, cymbium.

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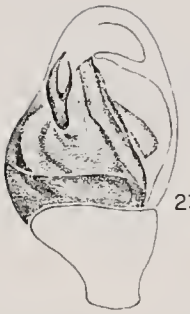
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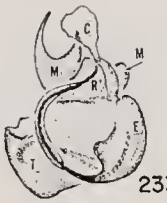

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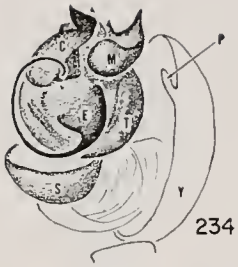

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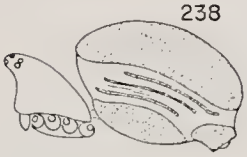
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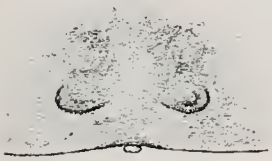
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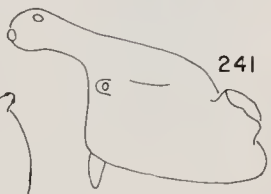
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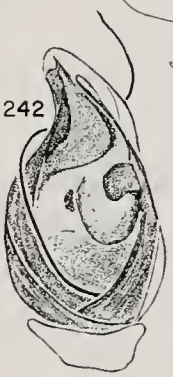
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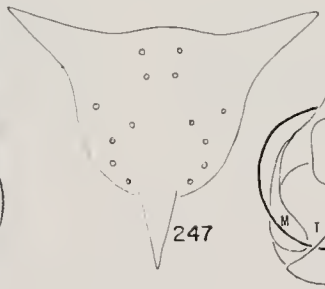
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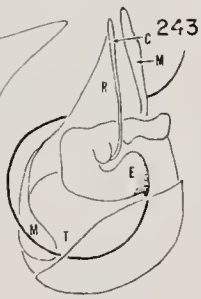

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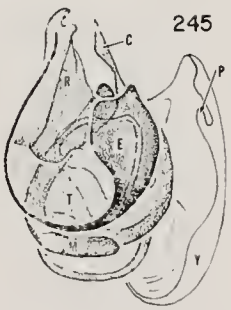

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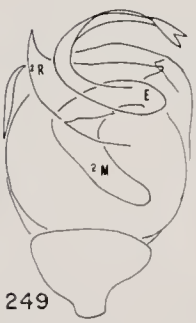

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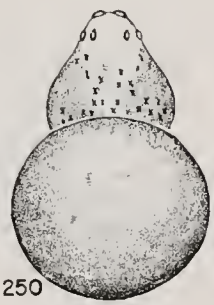
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THEONOE Simon

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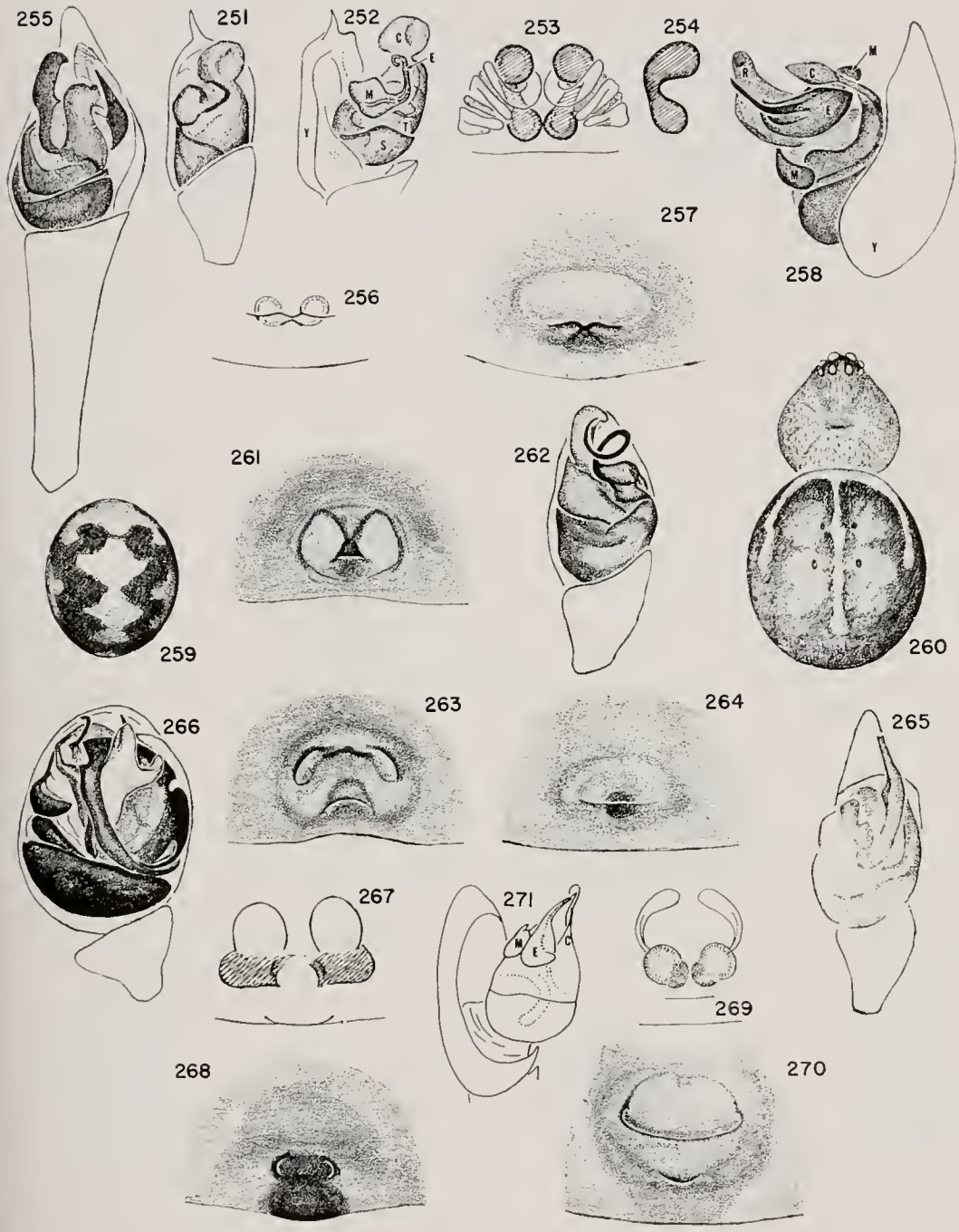
Abbreviations. C, conductor; E, embolus; M, median apophysis; R, radix; S, subtegulum; T, tegulum; Y, cymbium.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Icona Forster

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Abbreviations. C, conductor; E, embolus; M, median apophysis; P, paracymbium; R, radix; S, subtegulum; T, tegulum; Y, cymbium.

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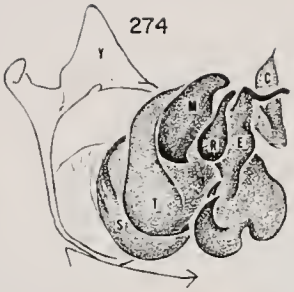
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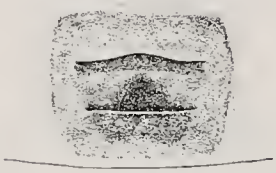
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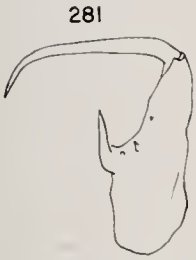
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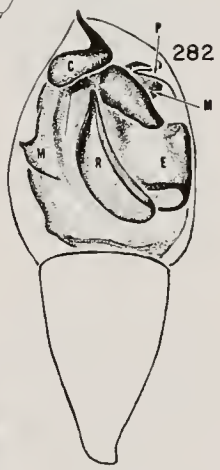
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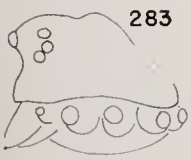
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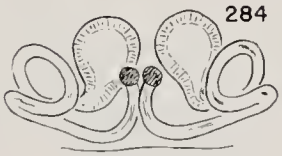
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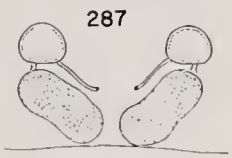
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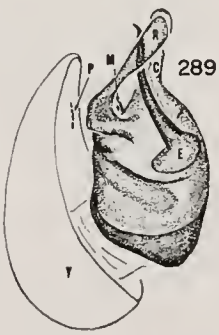
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Robertus O.P.-Cambridge

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Comaroma Bertkau

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Synotaxus Simon

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Argyrodes Simon

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Fig. 301. *A. projiciens* (O.P.-Cambridge), male carapace and chelicera.

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Fig. 304. *A. attenuatus* (O.P.-Cambridge), female.

Fig. 305. *A. draeus* Chamberlin and Ivie, female abdomen, lateral view.

Abbreviations. C, conductor; E, embolus; M, median apophysis; P, paracymbium; R, radix; S, subtegulum; T, tegulum; Y, cymbium.

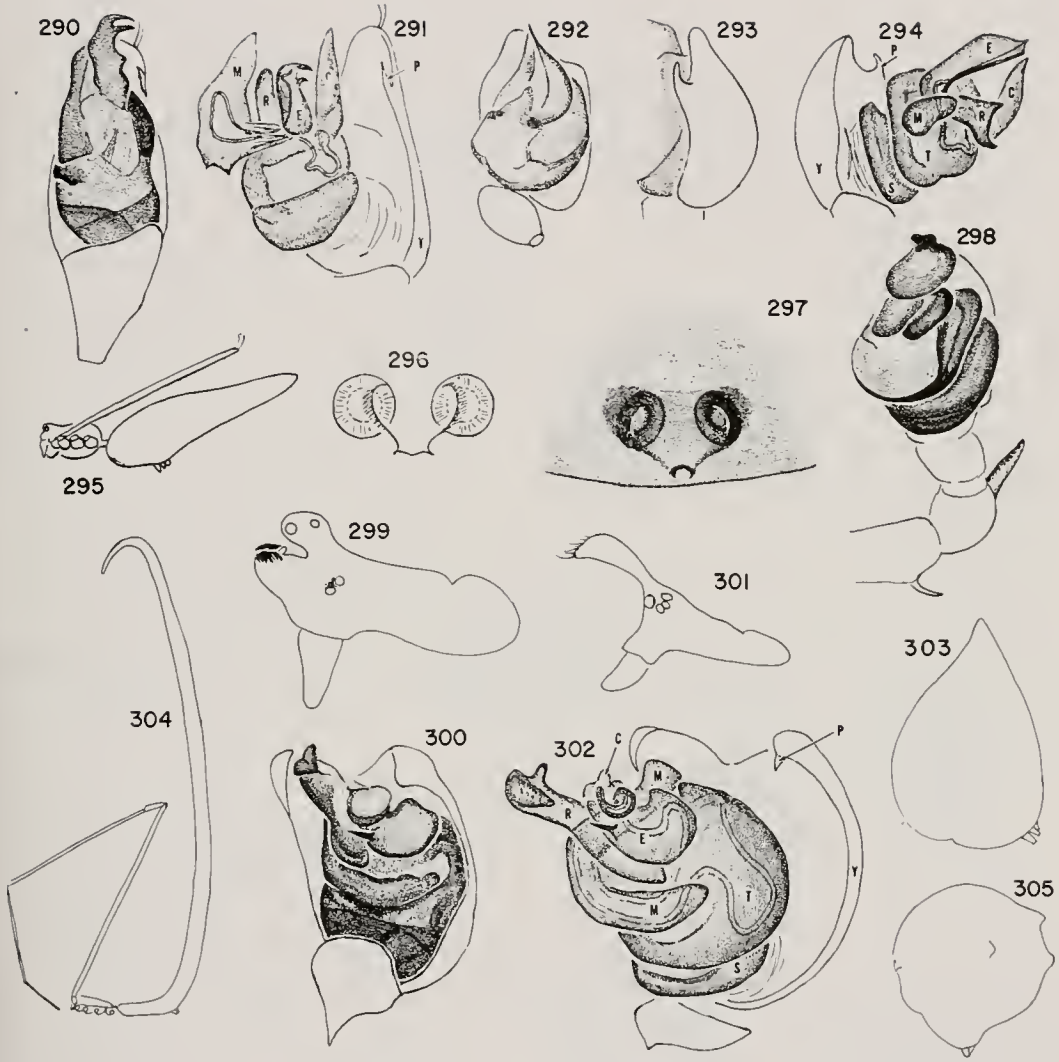
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Fig. 306. *Sedasta ferox* Simon, juvenile carapace and chelicerae.

Fig. 307. *Perania pallida* Thorell, juvenile, chelicera, frontal view (free-hand drawing).

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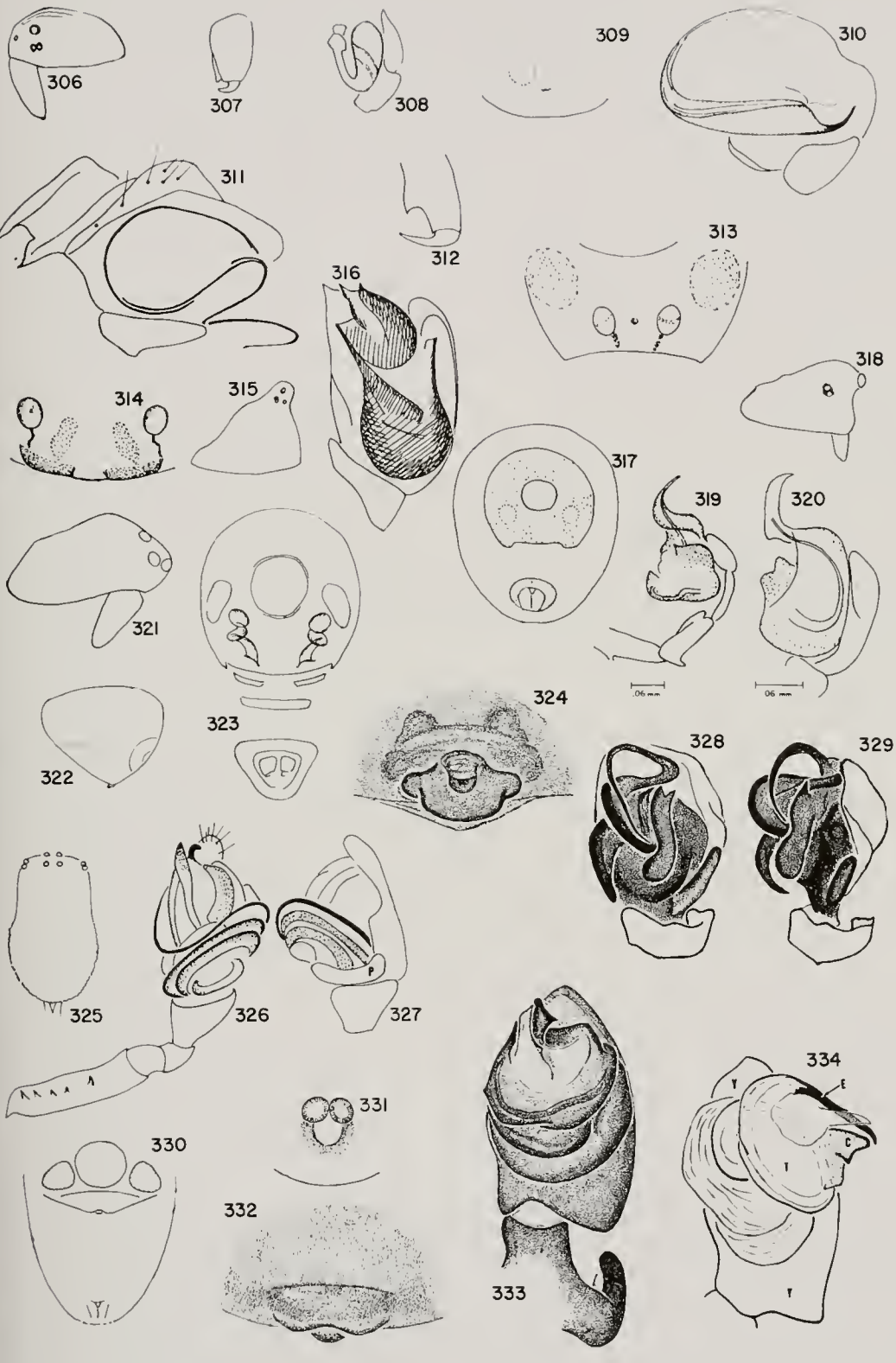
Abbreviations. C, conductor; E, embolus; P, paracymbium; T, tegulum; Y, cymbium.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Bulletin of the Museum of Comparative Zoology

AT HARVARD COLLEGE

VOL. 127, NO. 2

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AMERICAN SPIDERS OF THE GENUS ARGYRODES (ARANEAE THERIDIIDAE)

BY HARRIET EXLINE AND HERBERT W. LEVI

WITH FIFTEEN PLATES

CAMBRIDGE, MASS., U.S.A.
PRINTED FOR THE MUSEUM
MAY 25, 1962

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MUSEUM OF COMPARATIVE ZOOLOGY AT HARVARD COLLEGE

Bulletin (octavo) 1863 — The current volume is Vol. 127.

Breviora (octavo) 1952 — No. 156 is current.

Memoirs (quarto) 1864–1938 — Publication was terminated with Vol. 55.

Johnsonia (quarto) 1941 — A publication of the Department of Mollusks. Vol. 4, no. 40 is current.

Occasional Papers of the Department of Mollusks (octavo) 1945 — Vol. 2, no. 28 is current.

Proceedings of the New England Zoological Club (octavo) 1899–1948 — Published in connection with the Museum. Publication terminated with Vol. 24.

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No. 2 — *American Spiders of the Genus Argyrodes* (*Araneae, Theridiidae*)

By Harriet Exline[1] and Herbert W. Levi

Spiders of the genus *Argyrodes* are mostly tropical and subtropical. Some, perhaps all, live as commensals in webs of larger spiders, especially in webs of *Nephila clavipes* (Linnaeus) and species of *Gasteracantha* and *Argiope,* and sometimes of *Latrodectus, Agelenopsis, Allepeira* and others. Often large numbers of individuals, sometimes including more than one species, are found in the same host web. Twenty-three specimens including *A. elevatus, A. cochleaforma* and *A. cordillera* were collected from one *Gasteracantha* web near Baños, Ecuador (Exline, 1945). A pair of *A. globosus* and a pair of *A. cancellatus* were collected by Exline in a web of *Nephila clavipes* near Donaldsonville, Louisiana, in 1959. *Argyrodes* usually feed on small insects in the host web, the small spiders and small insects apparently being unnoticed by the large host. However, *Argyrodes* have been observed a few times to prey on their hosts. Exline watched *A. fictilium* feed on its *Araneus* host, and Archer (1946) reported *A. fictilium* preying on *Frontinella communis* (Hentz) in Alabama. Lamore (1958) observed *A. trigonum* attack and feed on a host *Allepeira lemniscata* (Walckenaer). *Argyrodes* may live in host webs without constructing any web of their own, but often they add fine lines between the spirals of an orb-web, and occasionally they live independently, making their own small theridiid webs.

Argyrodes species hang in the web upside-down with the front pairs of legs folded. They are usually inconspicuous, resembling seeds, pieces of bark, or lichen accidentally attached to the web. When disturbed they jump, usually sideways, and drop, leaving a line attached to the resting place.

Though the egg-cases are far more conspicuous than their makers, they are seldom preserved by collectors. They are beautifully constructed (Figs. 1-5) and are attached to the host web or to grasses or brush by strong threads. The shape is often characteristic. Urn-shaped cases are made by *A. elevatus, A. caudatus, A. cancellatus* (Fig. 5) and their relatives, and these

1 Mrs. D. L. Frizzell, Rolla, Missouri; Research Associate, California Academy of Sciences.

cannot be distinguished. Several egg-cases with a female *A. fictilium* (collected by W. J. Gertsch, W. Ivie, and T. B. Kurata in Ontario) included two or three oval-shaped, one elongate, one nearly round, and one spindle-shaped. The attractive spindle-shaped egg-cases of *A. projiciens* (Fig. 1) have been collected by A. M. Chickering, H. Exline and others. A very long, purse-like egg-case, filled with young spiderlings, was collected with a female *A. attenuatus* by A. M. Chickering in Panama (Fig. 3). The slightly elongate, urn-shaped egg-case of *A. trigonum* has been known since Emerton's figures of it were published in Hentz (1875); it is somewhat variable. The cases of its relative *A. baboquivari,* collected in Arizona by W. J. Gertsch, are similar but larger (Fig. 2).

Males of many species of *Argyrodes* have bizarre projections or other modifications of head and clypeus. Nearly all forms bear humps on the abdomen, or the abdomen is extended beyond the spinnerets. In a few species of the *Ariamnes* group, the abdomen is so greatly prolonged as to be vermiform. It may also be movable, perhaps camouflaging the spider as an inch-worm. The abdomen of *A. trigonum* and its relatives is also extended and can be moved up or down or sideways. In many species the abdomen is dull and spotted, in others black to reddish, streaked or studded with brilliant silvery spots, or in a few species nearly all silvery.

This revision has attempted to clarify the taxonomy of *Argyrodes.* There are keys, and a description of each species, with figures and a brief diagnosis, to help in identification. Distribution maps and records of available collections are included.

We include *Rhomphaea* and *Ariamnes* in *Argyrodes,* though with some misgivings due to resultant changes in nomenclature. Simon (1893) placed all three genera in the group (subfamily) Argyrodeae, separated by differences in eye arrangement, clypeal modification and relative length of metatarsi. We have found that these characters do not separate American species. Usage of the three generic names, moreover, shows considerable confusion. Many of the larger *Argyrodes* have been described as *Rhomphaea,* and species have been placed indiscriminately into either *Ariamnes* or *Rhomphaea. Argyrodes fictilium,* which is close to the type species of *Rhomphaea,* probably is closer to the *Ariamnes* group than are the other American species of *Rhomphaea.* The genitalia of the *Ariamnes* group are structurally very similar to those of the *Argyrodes argyrodes* group of species. Characters that separate *Rhomphaea-Ariamnes* from *Argyrodes* would fragment the

latter group also. We have, therefore, divided *Argyrodes* into species groups on the basis of head and clypeus shape of the male and shape of abdomen and genitalia, rather than into subgenera, which would add to the nomenclatural burden.

The revision is based on several large collections and many smaller ones made available to us through the kindly cooperation of individuals and museums. The most important collection, from Panama, was contributed by Dr. A. M. Chickering, who also provided a splendid collection from Jamaica (deposited in the Museum of Comparative Zoology). Dr. W. J. Gertsch lent us the large collection in the American Museum of Natural History. The collection of the Museum of Comparative Zoology added specimens and data from the eastern United States and the West Indies, and Exline's collection supplied material from Peru, Ecuador, and the midwestern United States. Other collections of importance include that of the California Academy of Sciences from western South America, lent by Dr. E. S. Ross; the British Museum (Natural History), lent by Dr. G. Owen Evans and D. Clark; the Muséum National d'Histoire Naturelle, Paris, lent by Prof. M. Vachon; the Senckenberg Museum, lent by Dr. O. Kraus; the Institut Royal des Sciences Naturelles de Belgique, lent by Mr. J. Kekenbosch; the University of Utah, lent by Dr. R. V. Chamberlin; and the Zoologische Sammlungen des Bayrischen Staates, lent by Dr. W. Engelhardt; and smaller collections by Dr. A. F. Archer and Mr. J. Beatty.

Our identification of species is based on examination and comparison with type specimens wherever possible. Examination of types in European institutions by H. W. Levi, during the summer of 1958, was made possible through the sponsorship of the National Science Foundation (Grant no. G-4317), and through the hospitality of Prof. M. Vachon of Paris, Dr. G. Owen Evans and Mr. E. Browning of London, and Prof. G. C. Varley of Oxford. Other types were made available by Dr. W. J. Gertsch, American Museum of Natural History; Prof. A. Petrunkevitch, Yale University; Dr. R. V. Chamberlin, University of Utah; Prof. M. Birabén, Museo de La Plata, Argentina; Dr. A. Riedel and J. Prózyński, Polish Academy of Sciences, Warsaw; Dr. L. Forcart, Naturhistorisches Museum, Basel; Dr. P. E. Vanzolini and Dr. H. de A. Camargo, Departamento de Zoologia da Secretaria da Agricultura, São Paulo, Brazil; and the Zoological Institute of Bologna. Dr. Patricio Sanchez, Universidad Catolica de Chile obtained a rare publication for us. Susan Kinnaird and Lorna Levi helped with editing the paper. Funds for the completion of

this study were supplied by the National Institutes of Health (Grant no. E-1944).

In this paper, literature records were used only in the few cases in which there was no doubt about their correct determination. Experience has demonstrated that a large proportion of spider names used in regional lists are misapplied and that the distributions summarized in catalogs are often erroneous. In our list of records the following abbreviations were used for European museums from which specimens were borrowed: BMNH, British Museum (Natural History); ISNB, Institut Royal des Sciences Naturelles de Belgique, Brussels; MNHN, Muséum National d'Histoire Naturelle, Paris; SMF, Senckenberg Museum, Frankfurt; ZSM, Zoologische Sammlungen des Bayrischen Staates, Munich.

Argyrodes Simon

Ariadne Doleschall, 1857, Nat. Tiidschr. Nederland Ind., vol. 13, p. 410. Type species by monotypy *A. flagellum* Doleschall, 1857. Homonym of *Ariadne* Horsfield, 1826; *Ariadne* Agassiz, 1845.

Argyrodes Simon, 1864, Histoire Naturelle des Araignées, first edit., p. 253. Type species by tautonymy *Linyphia argyrodes* Walckenaer. Homonym of *Argyrodes* Guenée, 1845.

Ariamnes Thorell, 1869, Nova Acta Reg. Soc. Sci. Uppsala, ser. 3, vol. 7, p. 37. New name for *Ariadne* Doleschall, 1857, preoccupied.

Rhomphaca L. Koch, 1872, Die Arachniden Australiens, pt. 1, p. 289. Type species by monotypy *R. cometes* L. Koch, 1872.

Conopistha Karsch, 1881, Berliner Ent. Zeitschr., vol. 25, p. 39. Type species by original designation and monotypy *C. Bona Dea* Karsch, 1881.

Faiditus Keyserling, 1884, Die Spinnen Amerikas, Theridiidae, pt. 1, p. 158. Type species designated by Petrunkevitch, 1928, Trans. Connecticut Acad. Sci., vol. 29, p. 118, *Faiditus ecaudatus* Keyserling, 1884.

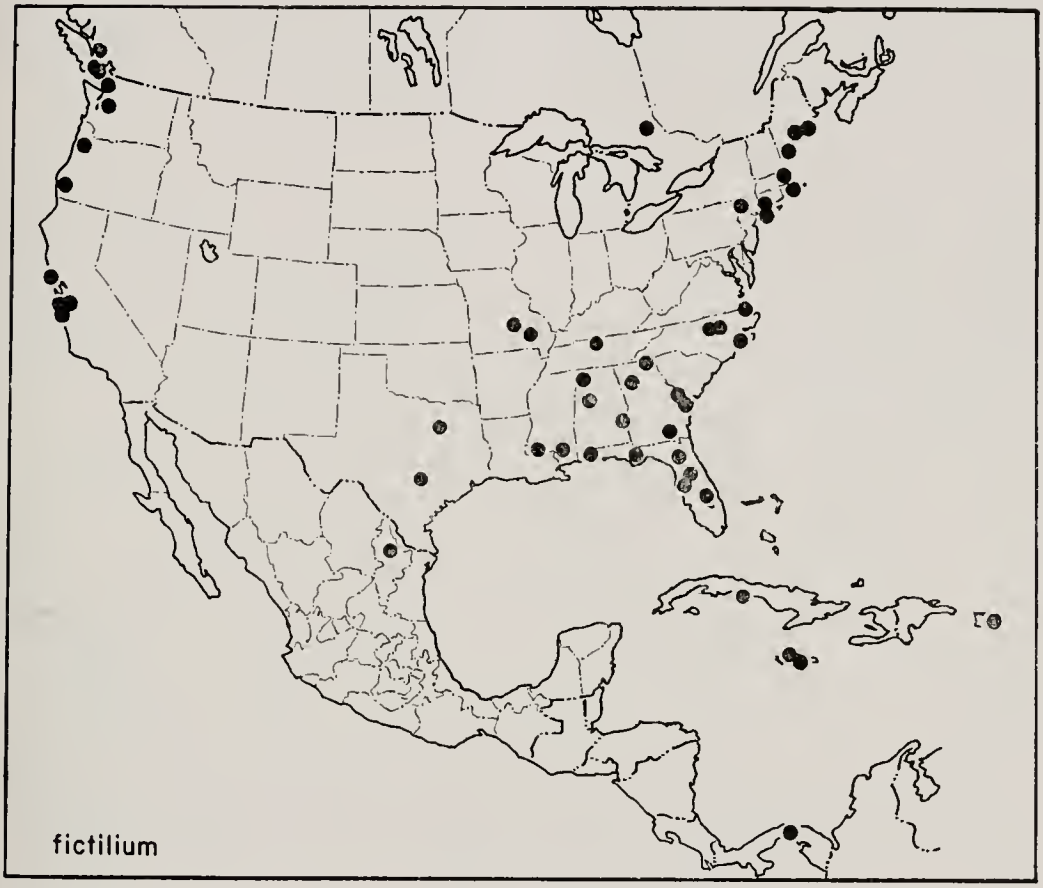
Bellinda Keyserling, 1884, *op. cit.*, p. 216. Type species by monotypy *Theridion cancellatum* Hentz.

Argyrodina Strand, 1928, Arch. Naturgesch., vol. 92, p. 42. New name for *Argyrodes* Simon, 1864, preoccupied.

Neospintharus Exline, 1950, Studies Honoring T. Kincaid, Univ. Washington Press, p. 112. Type species by original designation and monotypy *N. parvus* Exline, 1950.

Comments on nomenclature. Although the purpose of the International Rules of Nomenclature is to provide stability and universality of names, strict application of the rules often would work otherwise. The name of the genus revised in this paper is

an example. Because of the importance of stability, we have decided to use the generic name *Argyrodes,* although it is preoccupied by an older, unused homonym. An application to the International Commission on Zoological Nomenclature is being prepared to suppress the senior homonym of *Argyrodes.*

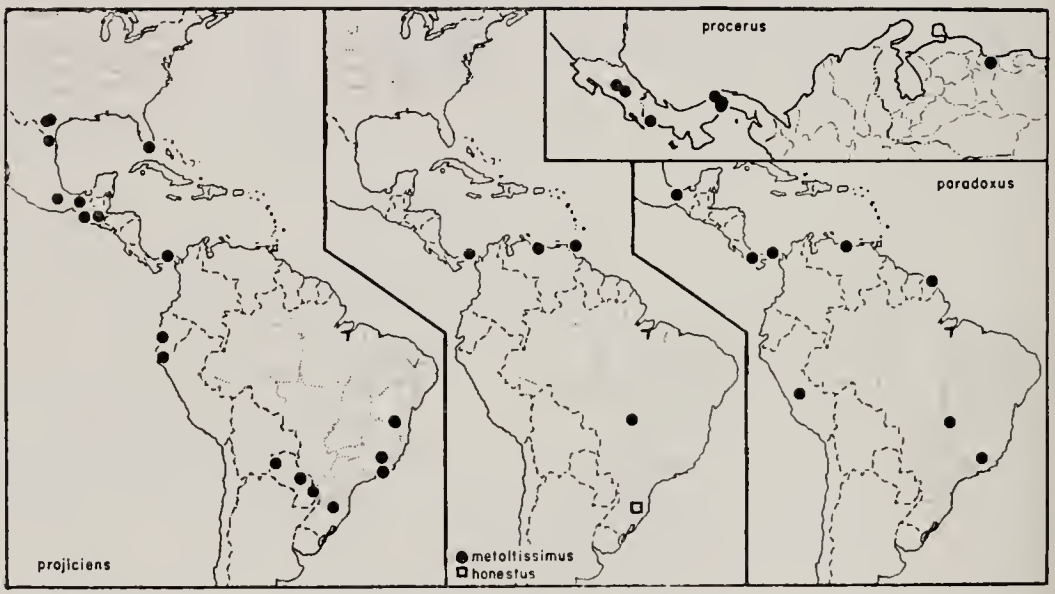


Map 1. Distribution of *Argyrodes fictilium* (Hentz).

Strand (1928) noted that *Argyrodes* was preoccupied and proposed the new name *Argyrodina. Argyrodes,* however, continued to be used for spiders until the 1930's. At that time *Conopistha* Karsch, 1881, with the type *C. bonadea* Karsch was recognized as a synonym of *Argyrodes,* and *Conopistha* has generally been used for this genus during the last 20 years. We now consider *Ariamnes* and *Rhomphaea,* both proposed before *Conopistha,* to be synonyms of *Argyrodes.* If we follow strictly the laws of priority the genus should be called *Ariamnes.* However, those who disagree with our synonymy may still consider *Conopistha* the correct generic name. Of the two recent catalogers,

Roewer uses *Argyrodina* (in his last volume he points out that *Conopistha* should have been used); Bonnet employs *Argyrodes*, strongly favored by usage.

The senior homonym *Argyrodes* Guenée, 1845, a moth of the family Perlididae, is a junior objective synonym of *Eucarphia* Huebner, 1825. *Argyrodes* Guenée is monotypic, the only species being *vinetella* Fabricius. *Eucarphia* Huebner contains three species, of which *vinetella* Fabricius is the type. Thus the name will not be available for a lepidopteran genus.[2]



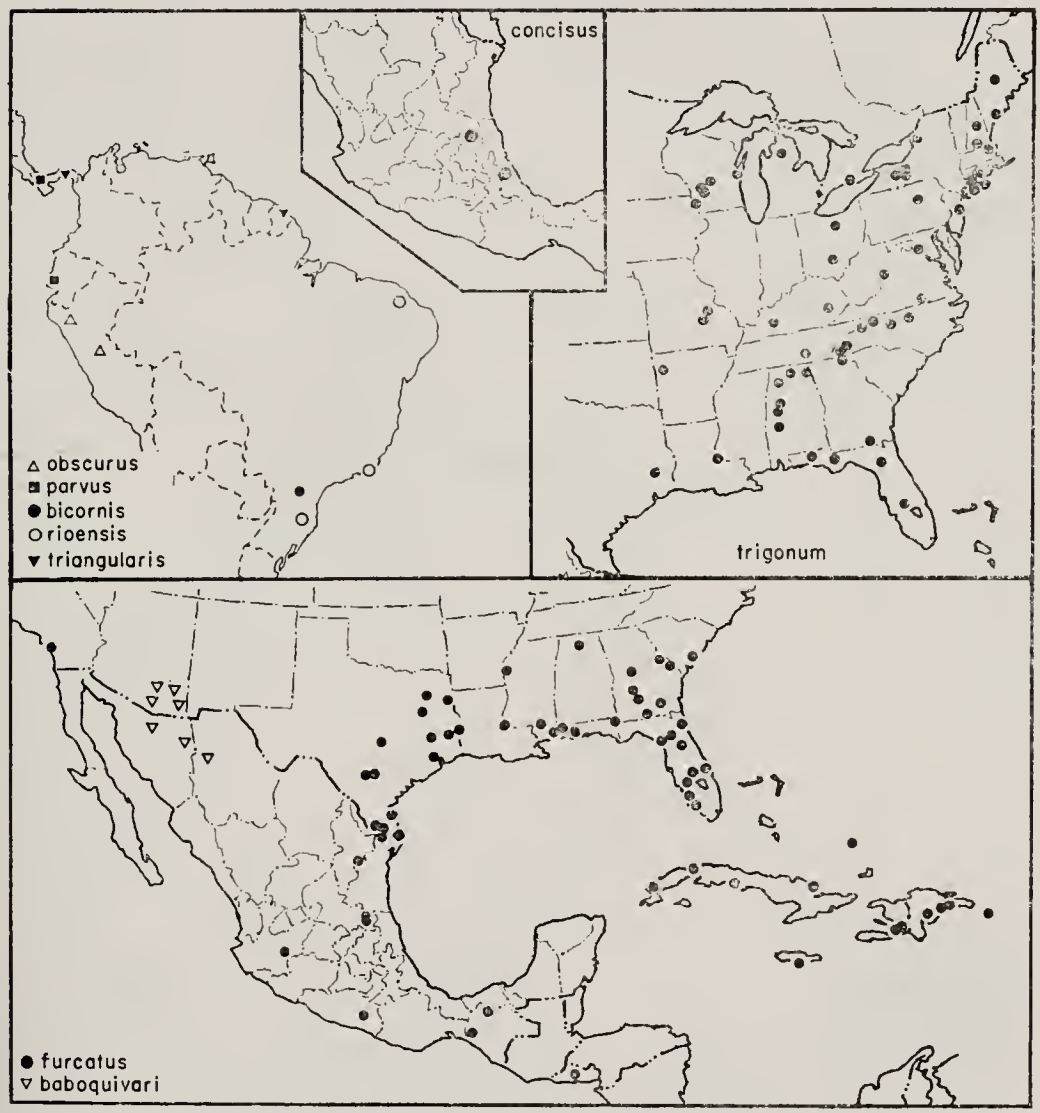
Map 2. Distribution of *Argyrodes honestus* new species, *A. metaltissimus* (Soares and Camargo), *A. paradoxus* Taczanowski, *A. procerus* (O.P.-Cambridge), and *A. projiciens* (O.P.-Cambridge).

Usage and continuity of names strongly favor *Argyrodes*. The alternate choice would be *Ariamnes*, which has been used before for only a small group of poorly known species. Its synonymy, moreover, is to some extent a matter of opinion, so that its use might lead to instability.

Description. Carapace flat, posterior portion low, a transverse thoracic depression generally present. Eye region and clypeus high. Males with eye region, or clypeus, or both, modified with projections, humps, an open groove or seam below eyes, or with clypeus projecting ventrally (*A. fictilium*), or projecting and bearing a groove (*A. atopus*). Color generally uneven brownish

[2] Information supplied by Prof. W. T. M. Forbes and Dr. E. G. Monroe.

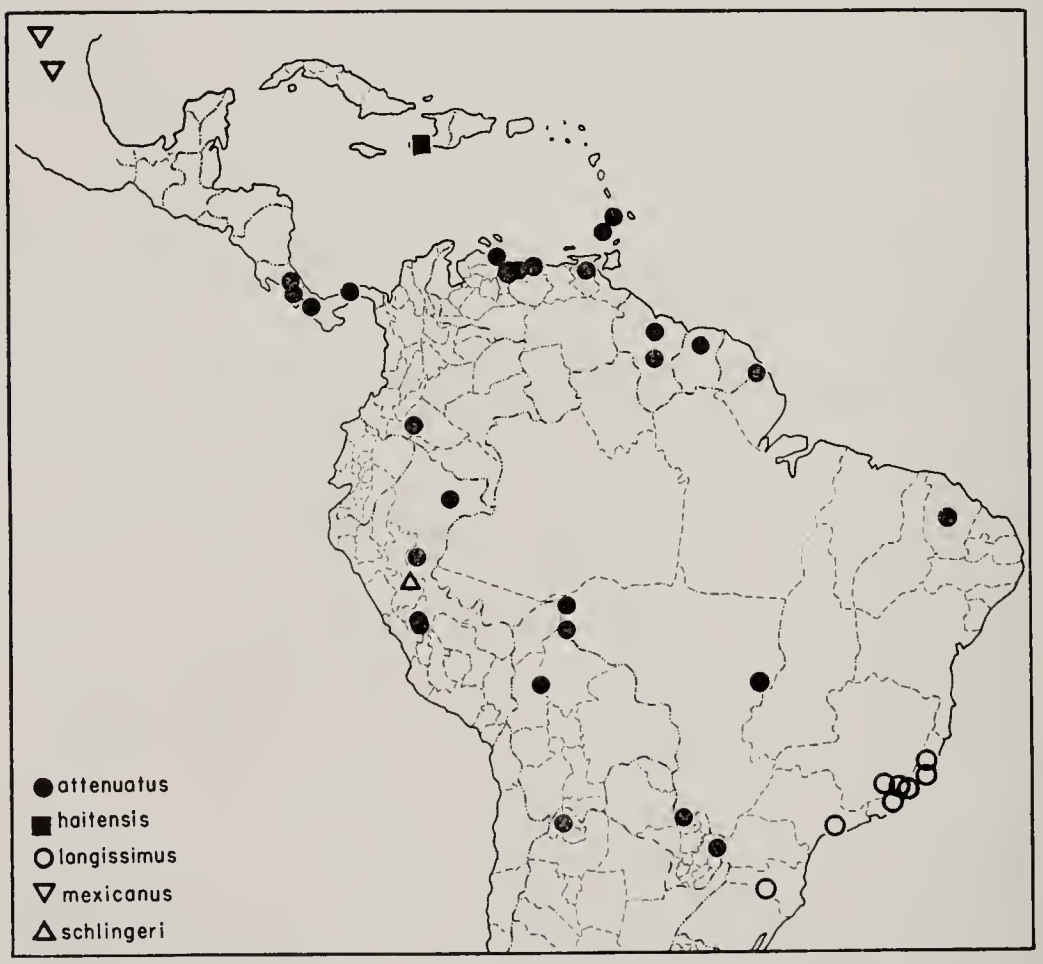
with irregularly distributed pigment. Chelicerae with two or three teeth on anterior margin, one or two posterior (Fig. 76), or a row of equal-sized denticles (each one with diameter less than one-quarter that of teeth). Sternum and lip entire. First leg longest, fourth second in length, third always very short. Fourth tarsus usually without a comb, but with a few serrated bristles. *Argyrodes attenuatus* has serrated bristles on the prolateral side of the distal end of the tarsus. Comstock (1912, The Spider Book, Doubleday, Page & Co., fig. 324) illustrates a few



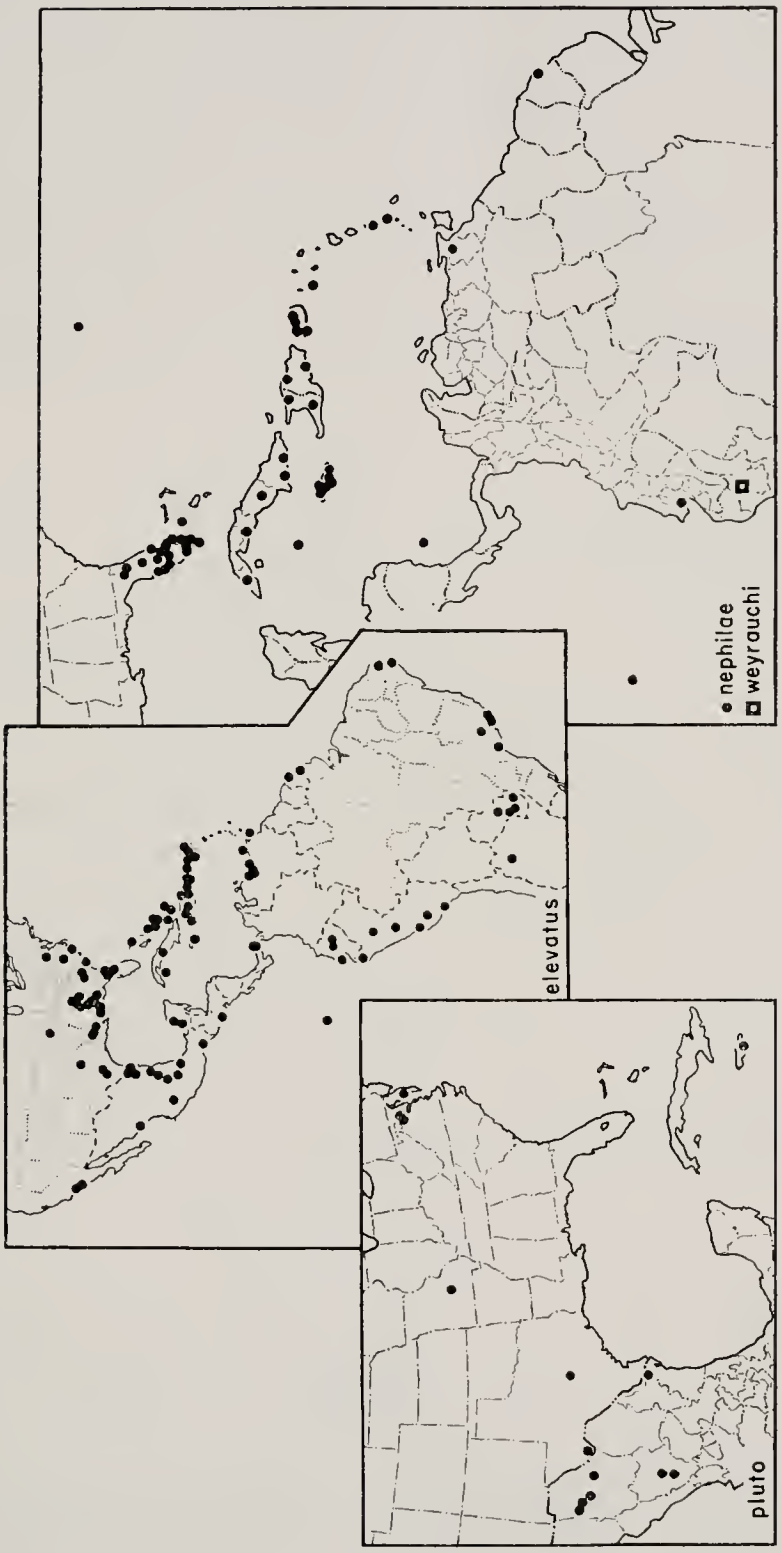
Map 3. Distribution of *Argyrodes baboquivari* new species, *A. bicornis* O.P.-Cambridge, *A. concisus* new species, *A. furcatus* (O.P.-Cambridge), *A. obscurus* Keyserling, *A. parvus* (Exline), *A. rioensis* new species, *A. triangularis* Taczanowski, and *A. trigonum* (Hentz).

serrated bristles on the side of the distal end of the tarsus of *A. trigonum*. The tarsal comb, when present in other theridiids, is on the venter. Also unlike other theridiid spiders, the middle tarsal claw is longer than the lateral claws. Abdomen with tubercles, extended, vermiform, or sometimes higher than long, never spherical (except in males of *A. globosus*). Anterior border of abdomen with stridulating ridges in both sexes and a pair of stridulating areas on carapace. The small colulus has the setae shorter than the fleshy base (Fig. 77). Abdomen with uneven coloration, often with silvery patches or all silvery.

Palpi with median apophysis (M in Figs. 68, 120, 154, 406, 407), radix (R), conductor (C). The duct loops through the inconspicuous, weakly sclerotized median apophysis. The latter structure fits into the paracymbium (P). The radix may be an



Map 4. Distribution of *Argyrodes attenuatus* (O.P.-Cambridge), *A. haitensis* new species, *A. longissimus* (Keyserling), *A. mexicanus* new species, and *A. schlingeri* new species.



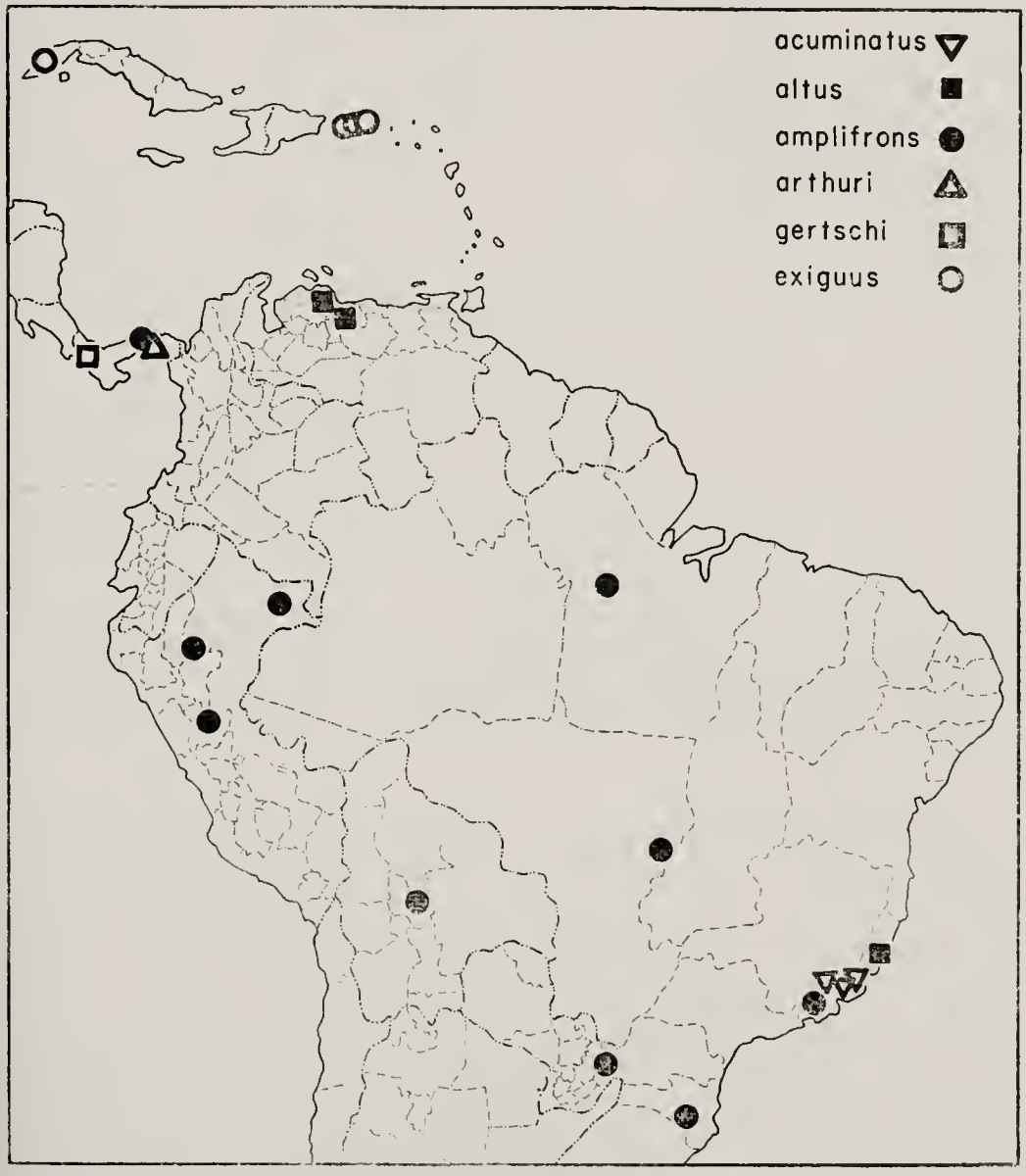
Map 5. Distribution of *Argyrodes elevatus* Taczanowski, *A. nephilae* Taczanowski, *A. pluto* Banks, and *A. weyrauchi* new species.

armlike sclerite between the embolus and the eymbium (Y) (Figs. 68, 120, 154), or a prominent ventral plate above the median apophysis (Figs. 406, 407). It is always sclerotized and is of diagnostie value, but often is partly transparent so that its outline is hard to see. The embolus is variously shaped: a complex selerite in some speeies of the *Ariamnes* and *A. argyrodes* groups (Figs. 120, 154); subtriangular in the *A. trigonum* group (Fig. 68); or with a distal thread-shaped portion in the *A. cancellatus* group (Figs. 406, 407). In the latter group, the embolus is partially hidden by the ventral radix. The eymbium is usually spoon-shaped, but is truncate in some *Ariamnes* and in all species of the *A. argyrodes* group (Fig. 154).

Map 6. Distribution of *Argyrodes atopus* Chamberlin and Ivie, *A. cochleaforma* (Exline), *A. cordillera* (Exline), *A. ecaudatus* (Keyserling), *A. fulvus* new species, *A. proboscifer* (Exline), *A. rossi* new species, and *A. sullana* (Exline).

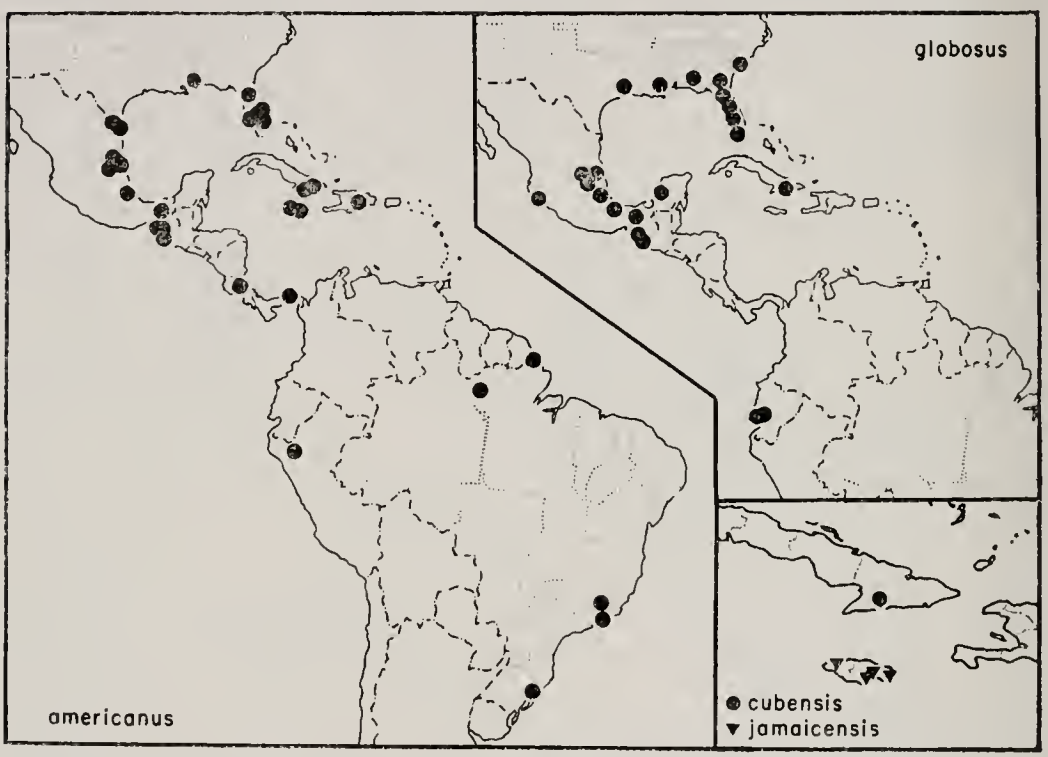
Epigynum a sclerotized plate, often covered by resinous material, which may be difficult to remove (except in the *A. cancellatus* group). Two spherical to oval receptacles, tube-shaped in the *Ariamnes* group. Ducts of variable length, generally of same diameter throughout. In some species of the *A. cancellatus* group the sclerotized ducts fuse.

In *Argyrodes* there is pronounced dimorphism of secondary sexual characters. Males may have setae-bearing projections in



Map 7. Distribution of *Argyrodes acuminatus* Keyserling, *A. altus* Keyserling, *A. amplifrons* O.P.-Cambridge, *A. arthuri* new species, *A. exiguus* new species, and *A. gertschi* new species.

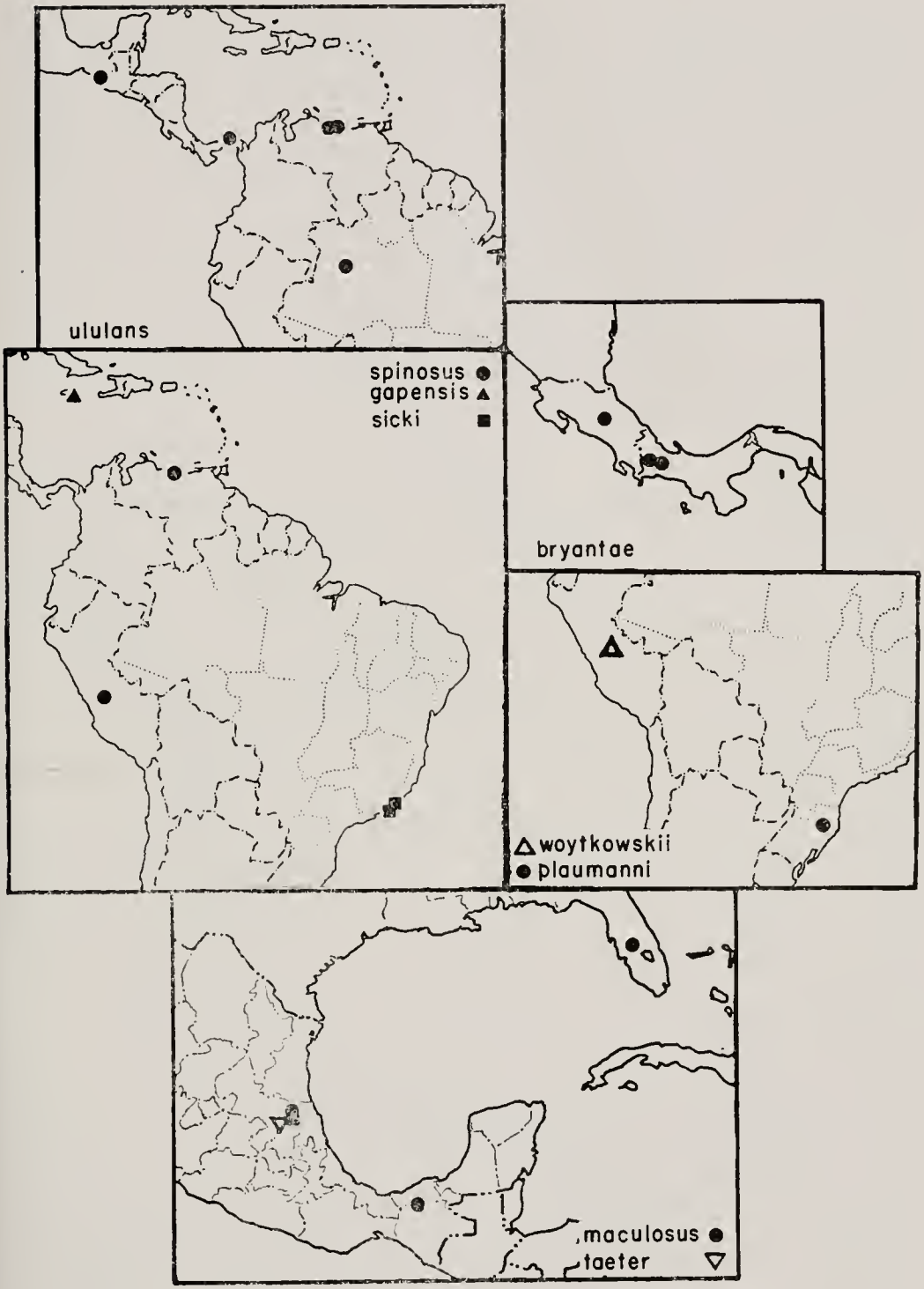
the eye region, clypeus, or both. In males the clypeus may be bulging, with a transverse seam, or may project below. The size and position of eyes often is different in females. The legs are usually considerably longer in males. Unlike most other theridiids, the males of many species are larger than the females, although the males are smaller in species of *Rhomphaea, Ariamnes,* and *A. trigonum* groups.



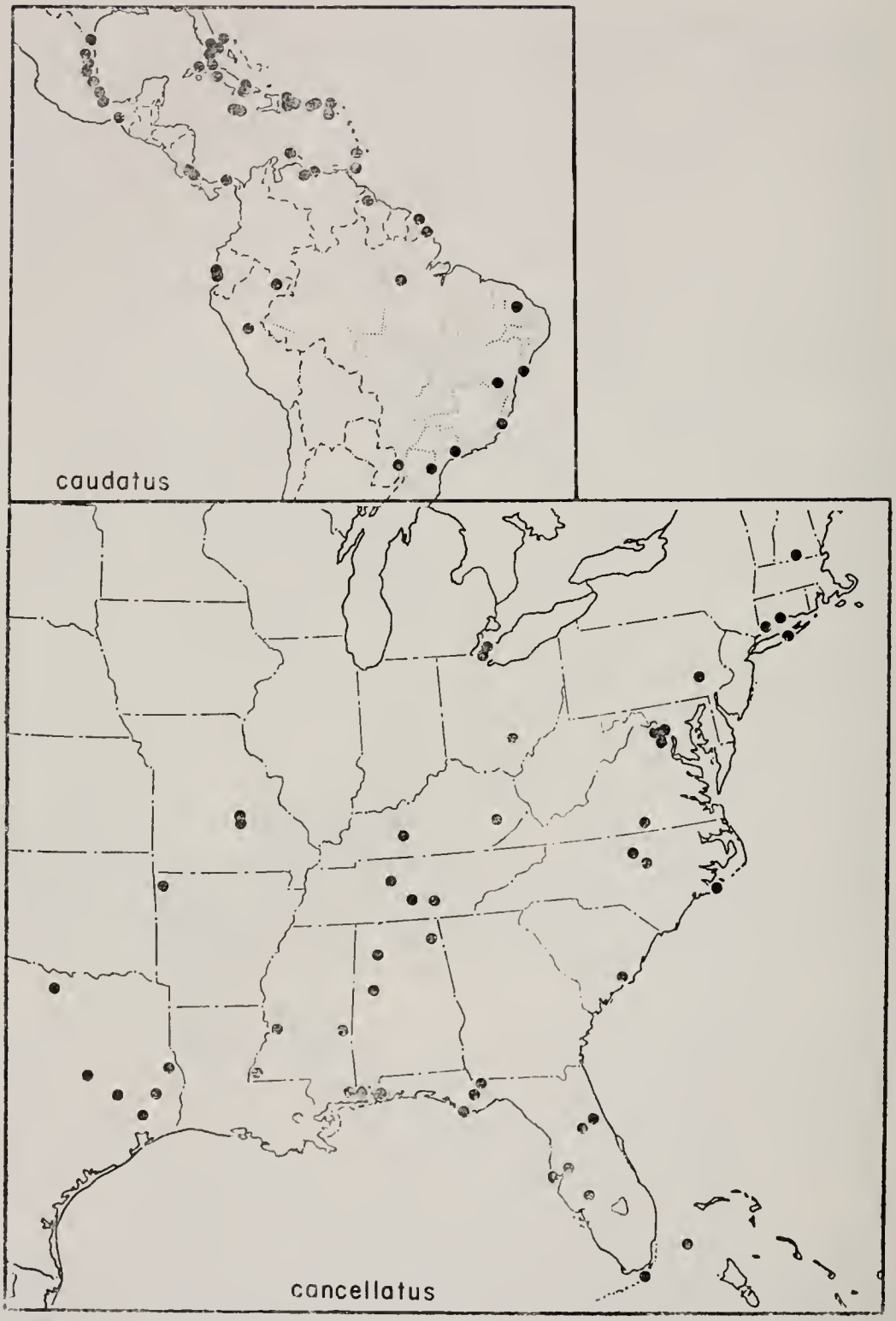
Map 8. Distribution of *Argyrodes americanus* (Taczanowski), *A. cubensis* new species, *A. globosus* Keyserling, and *A. jamaicensis* new species.

Diagnosis. Argyrodes differs from *Thwaitesia, Spintharus* and *Episinus* by the large size of the colulus, and by having one or two teeth on the posterior margin of the chelicerae. In *Thwaitesia, Spintharus* and *Episinus* the colulus is replaced by two setae and all three genera lack teeth on the posterior margin.

The relatively large colulus separates *Argyrodes* from *Thymoites,* which lacks a colulus; *Thymoites* males also have the eye region modified with projections. The modified head region of males, and the variously shaped (never oval) abdomen separates this genus from other Theridiidae with a large colulus: *Steatoda, Robertus,* and *Enoplognatha. Argyrodes* lacks the patellar spur of *Synotaxus* males.

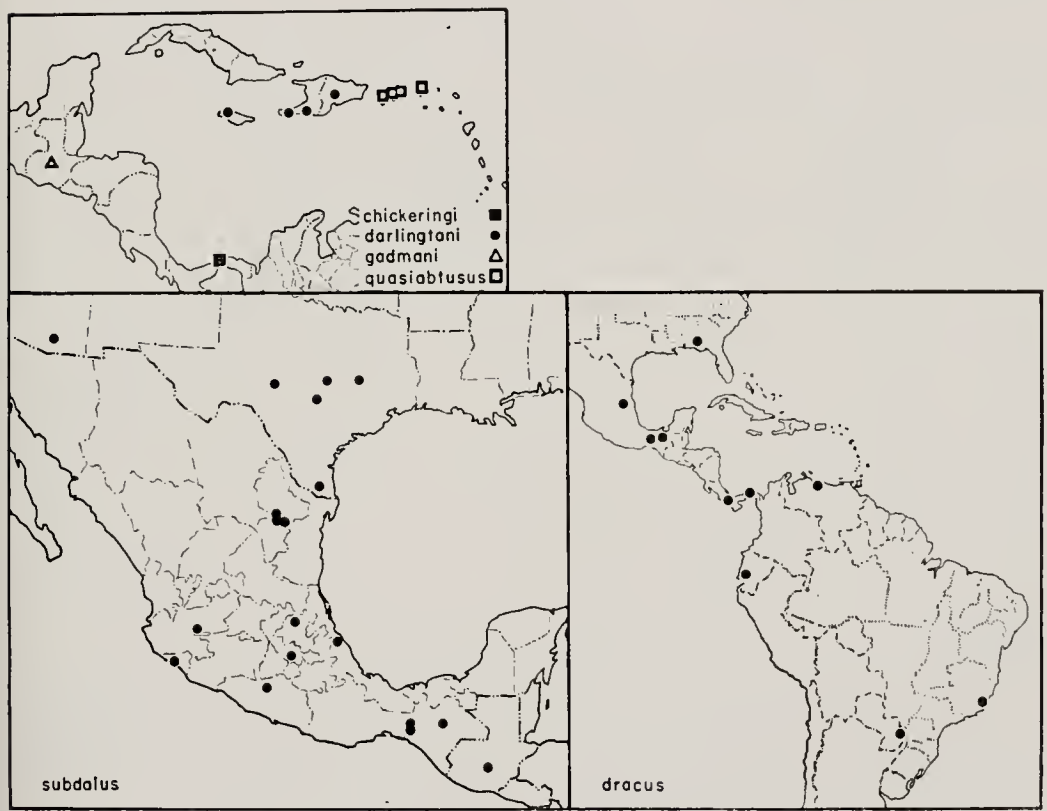


Map 9. Distribution of *Argyrodes bryantae* new species, *A. gapensis* new species, *A. maculosus* O.P.-Cambridge, *A. plaumanni* new species, *A. sicki* new species, *A. spinosus* Keyserling, *A. taeter* new species, *A. ululans* O.P.-Cambridge, and *A. woytkowskii* new species.



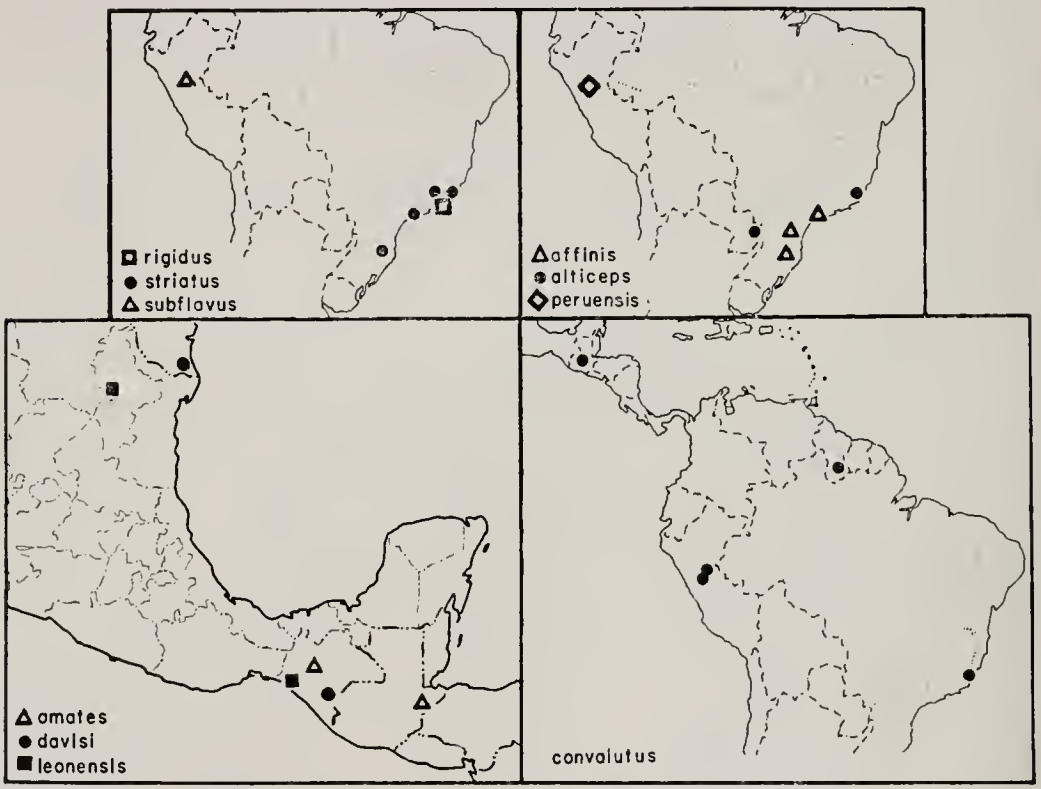
Map 10. Distribution of *Argyrodes cancellatus* (Hentz) and *A. caudatus* Taczanowski.

Distribution. *Argyrodes* species are common and widespread in tropical and warm regions of America and other parts of the world, but no species is known to be cosmotropical. Only one, *A. elevatus*, covers nearly the entire range of the genus in the Americas. Three species are found from southern Canada throughout the eastern United States: *A. fictilium*, *A. trigonum*, and *A. cancellatus*. *Argyrodes pluto* ranges from Maryland to western Mexico (Map 5). The western United States, except for the Southwest, is apparently devoid of *Argyrodes* except *A. fictilium*, which extends north along the Pacific coast to British Columbia, and *A. elevatus* and *A. furcatus*, which have been collected occasionally in southern California. *Argyrodes baboquivari* is the only species endemic to the southwestern United States and northwestern Mexico, although *A. pluto* and *A. subdolus* also occur. Several species are endemic to northeastern Mexico and southern Texas (*A. davisi*, *A. mexicanus*, *A. leonensis*, *A. tacter*,



Map 11. Distribution of *Argyrodes chickeringi* new species, *A. darlingtoni* new species, *A. dracus* Chamberlin and Ivie, *A. godmani* new species, *A. quasiobtusus* new species, and *A. subdolus* O.P.-Cambridge.

and *A. concisus*). Several species extend from southeastern United States to southern Brazil or Paraguay (*A. projiciens, A. elevatus, A. americanus, A. caudatus,* and *A. dracus*); several others extend from Central America to southern Brazil (*A. paradoxus, A. attenuatus, A. amplifrons*). Nineteen species have been collected in Panama. South American species are numerous but their ranges are inadequately known. Collections from most of the West Indies, Central and South America are too inadequate to support distributional generalities.



Map 12. Distribution of *Argyrodes affinis* O.P.-Cambridge, *A. alticeps* Keyserling, *A. amates* new species, *A. convolutus* new species, *A. davisi* new species, *A. leonensis* new species, *A. peruensis* new species, *A. rigidus* new species, *A. striatus* Keyserling, and *A. subflavus* new species.

Misplaced and Doubtful Species

Argyrodes elegans Taczanowski, 1872, Horae Soc. Ent. Rossicae, vol. 9, p. 118, pl. 5, fig. 11. Female type from Uassa [Amapa, Brazil], in the Polish Academy of Sciences, Warsaw, examined by Levi. [= *Chrysso elegans* (Taczanowski)].

Argyrodes floridana Banks, 1900, Canadian Ent., vol. 32, p. 98. Female syntypes from Punta Gorda, Florida, in the Museum of Comparative Zoology, examined by Levi. (= *Coleosoma acutiventer* Keyserling).

Argyrodes infelix O.P.-Cambridge, 1880, Proc. Zool. Soc. London, p. 340, pl. 30, fig. 18. Female type from the Amazon, in the Hope Department of Entomology, Oxford University, examined by Levi. [= *Helvibis infelix* (O.P.-Cambridge)].

Argyrodes longicaudatus Keyserling, 1891, Die Spinnen Amerikas, Brasilianische Spinnen, p. 209, pl. 8, fig. 150, ♀, ♂. Syntypes from Est. Rio de Janeiro, Brazil, in the British Museum, Natural History, examined by Levi. [= *Synotaxus longicaudatus* (Keyserling)].

Argyrodes lucmae Chamberlin, 1916, Bull. Mus. Comp. Zool., vol. 60, p. 228, pl. 15, figs. 4-6, ♂. Male type from Lucma, Peru, in the Museum of Comparative Zoology, examined by Levi. (Linyphiidae).

Argyrodes vittatus Keyserling, 1884, Die Spinnen Amerikas, Theridiidae, pt. 1, p. 191, pl. 9, fig. 114. Female types from Bogota, Colombia and Pumamarca, Peru, in the British Museum, Natural History, examined by Levi. [= *Chrysso vittatula* (Roewer)].

Argyrodina monoceros di Caporiacco, 1947, Monitore Zool. Italiano, vol. 56, p. 24. (? *nomen nudum*); 1948, Proc. Zool. Soc. London, vol. 118, p. 649, ♂ (sub *Conopistha*). Male type from British Guiana. [= *Synotaxus monoceros* (di Caporiacco)].

Argyrodina vittatula Roewer, 1942, Katalog der Araneae, vol. 1, p. 439. New name for *A. vittatus* Keyserling. [= *Chrysso vittatula* (Roewer)].

Conopistha acuminata Schenkel, 1953, Verh. Naturf. Gesell. Basel, vol. 64, p. 13. Female type from Prov. Falcon, Venezuela, in the Naturhistorisches Museum, Basel, examined by Levi. [= *Chrysso vittata* (O.P.-Cambridge)].

Conopistha monoceros (di Caporiacco), 1948, Proc. Zool. Soc. London, vol. 118, p. 649, figs. 57-59. [=*Synotaxus monoceros* (di Caporiacco)].

Faiditus bruneoviridis Mello-Leitão, 1948, An. Acad. Brasileira Cienc., vol. 20, p. 156. Female type from British Guiana. [= *Episinus bruneoviridis* (Mello-Leitão)].

Rhomphaea anomala Chamberlin and Ivie, 1936, Bull. Univ. Utah, biol. ser., vol. 3, no. 5, p. 41, fig. 50, ♀. Female type from Panama, in the University of Utah collection. (= *Synotaxus turbinatus* Simon).

The following is a doubtful name. The type is lost. The name may have been applied to a species in the genus.

Theridion intentum Hentz, 1850, Jour. Boston Soc. Nat. Hist., vol. 6, p. 278.

Species whose types were not available and whose description is insufficient for recognition:

Ariamnes feioi Mello-Leitão, 1947, Bol. Mus. Nac., Rio de Janeiro, n.s., zool., no. 80, p. 10, fig. 46. Female type from Rio Claro, Minas Gerais, Brazil, in the Museo Nacional, Rio de Janeiro, belongs to the *Rhomphaea* group.

Conopistha barrosi Mello-Leitão, 1951, Rev. Chil. Hist. Nat., vol. 51-53, p. 330, from Chile. This species is probably *Anelosimus attritus* (Nicolet).

C. friburgensis Mello-Leitao, 1943, An. Acad. Brasileira Cienc., vol. 15, p. 259, from Friburgo, Rio de Janeiro, Brazil. Female type in the Museo Nacional, Rio de Janeiro, is probably *A. elevatus*.

C. pickeli Mello-Leitão, 1943, *ibid.*, p. 259, from Tapera, Pernambuco, Brazil. Female type in the Museo Nacional, Rio de Janeiro, is probably *A. elevatus.*

Rhomphaea altissima Mello-Leitão, 1941, Arq. Inst. São Paulo, vol. 11, p. 249. Female type from Rio Negro, Paraná, Brazil, in the Museo Nacional, Rio de Janeiro, is probably *A. paradoxus.*

R. brasiliensis Mello-Leitão, 1919 (1920), Rev. Soc. Brasileira Scienc., no. 3, p. 174. Female type from Rio de Janeiro, Brazil, in the Museo Nacional, Rio de Janeiro, is probably *A. metaltissimus.*

Relationships. Unlike other large theridiid genera (e.g. *Theridion, Dipoena*), *Argyrodes* species are similar in structure and probably are closely related. The widest gap in structural affinity occurs between the *A. cancellatus* group and the others. In the male palpus of the *A. cancellatus* group, a prominent ventral radix hides most of the embolus. The embolus has a basal portion and a spiralling thread-like distal tube. A complicated terminal, partly fleshy conductor supports the tip of the tube (Figs. 406, 407). The male carapace usually lacks projections, but the clypeus has a horizontal seam or groove, and often bulges and may overhang the chelicerae (Figs. 178, 225). The abdomen is not usually extended far behind the spinnerets but is often modified with paired humps and short posterior projections (Figs. 180, 227). All other *Argyrodes* have the palpal radix, often armlike, lying in back between the embolus and the cymbium (Figs. 68, 120, 154), and the embolus is completely exposed in ventral view. The carapace generally bears projections in the eye region or on the clypeus, and the abdomen is usually extended far behind the spinnerets, and is without lateral humps.

The *Rhomphaea* group is characterized by a long projection in the eye region of males (Figs. 9, 12, 15, 24) (absent in *A. fictilium*), and an elongate, pointed abdomen (Figs. 27, 29, 32). The male genital structures of most species (Figs. 6, 11, 14) are similar to those of the *A. trigonum* group. The epigyna are often weakly sclerotized. In many species the palpal femora and tibiae are elongate. *Argyrodes fictilium* is similar to the others in shape of the abdomen and genital structures; however, the clypeus is slanting below (Fig. 7). Considerable variability is found within some species of this group of which representatives are found in other parts of the world. American species are widespread but rare (Maps 1, 2).

The *A. trigonum* group differs from the previous one in having a projection from the clypeus of the male, parallel to that of the eye region (Fig. 78); the abdomen is shorter, usually with two tubercles at the posterior tip (Figs. 69-73, 86, 91). The species

of this group are very similar. The shape of the male carapace and palpal radix are diagnostic. Females are hard to separate. The ducts of the internal genitalia are always short and similar. The width and length of the median raised area of the epigynum differ slightly in different species; however, the shape of the median raised area is somewhat variable in all species. All species have a limited distribution (Map 3), and none are known outside America.

Species of the *Ariamnes* group are characterized by an extremely long, vermiform abdomen (Figs. 99, 100, 127), low carapace, and elongate seminal receptacles in the female (Figs. 121-123) (short in *A. mexicanus*). Palpal structures are more variable. *Argyrodes longissimus* is similar to *A. paradoxus* of the *Rhomphaea* group; *A. mexicanus* to other species of the *Rhomphaea* and *A. trigonum* groups; and *A. attenuatus* is similar to species of the *A. argyrodes* group. The species are readily separated by their genitalia. Species belonging to this group are found in the tropics of all parts of the world. Their ranges do not overlap in America (Map 4).

Species of the *A. argyrodes* group also are very similar. Only four are American; probably there are many in other parts of the world. The anterior median eyes are borne on a cephalic projection that parallels a large clypeal projection (Figs. 128, 133). The palpal cymbium in all species is truncate, as in some species of the *Ariamnes* group. The embolus of the male palpus is a more complicated structure than in the previous groups, but its shape is not diagnostic. The radix differs in shape in different species (Figs. 129, 134, 139, 144). The epigynum is heavily sclerotized and has two large subcircular fossae. The seminal receptacles and tubes are simple, and are also heavily sclerotized. The females of some species are difficult to separate.

The three species placed in the *A. cordillera* group are of doubtful affinity. (The male of *A. fulvus* is unknown). *Argyrodes cordillera* has no clypeal or cephalic projections (Fig. 155); *A. rossi* has a short setae-bearing clypeal tubercle (Fig. 160). The position of the palpal sclerites is as in the *Rhomphaea* group, but they are more heavily sclerotized, and the embolus is corkscrew-shaped. The female epigynum has a posterior rather than an anterior rim (Figs. 159, 164, 167).

The *A. cancellatus* group (characterized above) has many closely related species, with only slight genitalic differences. Four species (*atopus, proboscifer, cochleaforma, sullana*) are set off

from the rest by an unusual projection of the clypeus at its ventral margin (Figs. 178, 183, 188, 194). Several close to *A. gertschi* have the palpal radix split (completely in *A. arthuri,* Fig. 200), and have large seminal receptacles with tubes entering anteriorly (Figs. 202, 209). The numerous species near *A. cancellatus* are, however, very similar with diagnostic differences in the position of the clypeal seam, the shape of the clypeus, and minor differences in palpal parts, especially in the shape of the radix. The portion of the radix near the median ventral edge is usually transparent, showing the embolus underneath. Due to this transparency the edge may be difficult to see. The embolus also may be diagnostic, but is partially hidden by the radix. Because many species are rare, it was not dissected and sufficiently studied in this revision. It is possible that clearing the palpus with clove oil (as was done for *A. globosus* and *A. americanus*) may reveal additional diagnostic characters in the embolus. The conductor may also be diagnostic. The epigyna of many species are very similar but the seminal receptacles and shape and position of the long ducts are often good diagnostic characters, as they differ greatly in otherwise similar species. Related species may also differ in the shape of the abdomen. America is probably far richer in species of this group than other parts of the world.

Key to species groups

1a. Abdomen vermiform, with parallel sides, more than 10 times as long behind as anterior to spinnerets, ending in a single tip (Figs. 99, 100); clypeus straight ..... *Ariamnes* group

1b. Abdomen short or tapering, not more than six times as long behind as anterior to spinnerets, or if longer, clypeus projecting below, or abdomen with four tips 2

2a. Males with a setae-bearing clypeal projection and a parallel cephalic projection or hump bearing setae but not eyes (Figs. 66, 79); epigynum with a longitudinal ridge bearing indistinct openings (Figs. 55, 75, 94); abdomen with two tips (Figs. 69-73) ..... *A. trigonum* group

2b. Males otherwise, or if with clypeal and cephalic projection, latter bearing eyes (Fig. 128); epigynum otherwise; abdomen with one to several tips 3

3a. Males with cephalic projection bearing eyes anteriorly and parallel clypeal projection (Figs. 128, 133); epigynum with two large subcircular or oval fossae (bordered all around except in *A. pluto* Fig. 142) on a raised, heavily sclerotized plate (Figs. 132, 137, 150), female ducts short (Figs. 131, 141); abdomen subtriangular with a single tip (Figs. 130, 135, 140) ..... *A. argyrodes* group

3b. Males otherwise, or if with two projections, cephalic projection bearing eyes on sides (only in *A. plaumanni* Fig. 168); epigynum otherwise, female ducts variable; abdomen variable 4

4a. Male carapace with a single cephalic projection (Figs. 9, 12, 24)), or if lacking, clypeus slanting and projecting below (Fig. 7); female abdomen tapering to a single tip usually crowned by one or more spines, four to six times as long behind as anterior to spinnerets (Figs. 26, 29, 36, 41) ..... *Rhomphaea* group

4b. Male carapace otherwise; female abdomen shorter behind than anterior to spinnerets, or if longer, not evenly tapering, with bulges on sides; usually with four tips, never crowned by spines 5

5a. Male clypeus without a transverse seam or ventral projection (Figs. 155, 160); palpal radix between embolus and cymbium (Figs. 156, 161); epigynum without scape, fossae without anterior border (Figs. 159, 164, 167) ..... *A. cordillera* group

5b. Male clypeus with a transverse seam (Figs. 261, 271, 323) or ventral projection (Fig. 178); palpal radix a large ventro-mesal sclerite hiding embolus (Figs. 129, 332); epigynum with scape, or if not, fossae with anterior border (Figs. 320, 336, 405) ..... *A. cancellatus* group

Key to the *Rhomphaea* group species

1a. Male eye region without projection (Fig. 7); epigynum with a central raised area, bordered on three sides (Fig. 28); North and Central America ..... *fictilium*

1b. Eye region of male with projection; epigynum otherwise 2

2a. Thread-shaped portion of embolus longer than length of cymbium (Fig. 23); cephalic projection of male carapace with dorsal tubercle (Fig. 24); epigynum slanting off posteriorly, slant bordered anteriorly by a lip, posteriorly by the genital groove (Figs. 46, 47, 49, 50) ..... *paradoxus*

2b. Thread-shaped portion of embolus shorter than cymbium length; cephalic projection without dorsal tubercle; epigynum flat without posterior slant 3

3a. Cephalic projection of male without swelling below distal bulge (Figs. 9, 12); epigynum lightly sclerotized, two openings of epigynum very difficult to see (Figs. 31, 34) 4

3b. Cephalic projection of male with a swelling below distal end (Figs. 15, 18); epigynum sclerotized with one conspicuous central fossa (Figs. 40, 43) 5

4a. Cephalic projection of male with distal rounded knob (Figs. 12, 13); epigynum with a faint sclerotized posterior border of variable shape (Fig. 34) ..... *procerus*

4b. Cephalic projection longest on ventral side (Figs. 9, 10); epigynum lacking faint posterior border (Fig. 31) ..... *projiciens*

5a. Cephalic projection widest at distal end with ventral setae-bearing tubercle (Fig. 15); fossa of epigynum with ducts leaving in a posterior direction (Fig. 43) ..... *honestus*

5b. Cephalic projection widest at swelling in middle, and lacking ventral tubercle (Figs. 17-22); fossa of epigynum with ducts leaving in a posterior-lateral direction (Figs. 38, 40) ..... *metaltissimus*

Key to the *A. trigonum* group species

Males

1a. Projection in eye region very small or absent (Fig. 79); Peru ..... *obscurus*

1b. Projection in eye region always present and distinct 2

2a. Clypeus projection very thick, separated from cephalic projection by less than its diameter (Fig. 51); Ecuador to Panama ..... *parvus*

2b. Projections separated distally by more than the diameter of clypeal projection 3

3a. Both projections short and stubby, in profile wider than long (Fig. 56); Mexico ..... *concisus*

3b. Clypeal projection always longer than wide in profile 4

4a. Clypeal projection about twice as long as wide (Figs. 84, 89) 5

4b. Clypeal projection at least two and one-half times as long as wide (Figs. 61, 66, 95, 97) 6

5a. Palpal radix wider than long, with a ventral tooth (Fig. 90); southwestern U.S.A., northwestern Mexico ..... *baboquivari*

5b. Radix longer than wide without ventral tooth (Fig. 85); southeastern U.S.A., Mexico, West Indies ..... *furcatus*

6a. Distance between eye and clypeal projection about as wide as clypeal projection (Fig. 66); eastern U.S.A. ..... *trigonum*

6b. Distance between eye and clypeal projection much wider 7

7a. Length of clypeal projection noticeably shorter than height of clypeus below projection (Fig. 61); eastern Brazil ..... *rioensis*

7b. Length of clypeal projection almost equal to height of clypeus below projections (Figs. 95, 97) 8

8a. Base of projections separated by more than length of clypeal projection (Fig. 95); southeastern Brazil ..... *bicornis*

8b. Base of projections separated by less than length of clypeal projection (Fig. 97); Panama, Guiana ..... *triangularis*

Females

1a. Median epigynal ridge about as wide as long (Figs. 83, 88, 93, 94) .. 2

1b. Median epigynal ridge much longer than wide (Figs. 55, 60, 65, 75) .. 4

2a. Peru ..... *obscurus*

2b. North America 3

3a. Connecting ducts short (Fig. 87), ridge 0.06 mm wide; eastern U.S.A., Mexico, West Indies ..... *furcatus*
3b. Connecting ducts long (Fig. 92), ridge 0.12 mm wide; southwestern U.S.A., northwestern Mexico ..... *baboquivari*
4a. Epigynum as in Fig. 75; eastern U.S.A. ..... *trigonum*
4b. Epigynum otherwise; not U.S.A. 5
5a. Epigynum as in Fig. 60; Mexico ..... *concisus*
5b. Epigynum otherwise; Central or South America 6
6a. Epigynum as in Fig. 55; Ecuador to Panama ..... *parvus*
6b. Epigynum as in Fig. 65; eastern Brazil ..... *rioensis*

Key to the *Ariamnes* group species

1a. Palpus with a large, prominent hook-shaped embolus (Figs. 102-105); epigynum with a flat transverse bridge (Fig. 109); southern Brazil .. *longissimus*
1b. Palpus, epigynum otherwise 2
2a. Palpal embolus diamond-shaped (Fig. 113); epigynum with an indistinct transverse ridge (Fig. 115), seminal receptacles suboval (Fig. 114); Mexico ..... *mexicanus*
2b. Palpal embolus not diamond-shaped; epigynum otherwise, seminal receptacles more than three times as long as wide 3
3a. Epigynum an indistinct transparent knob (Fig. 111), seminal receptacles folded back (Fig. 110); [male unknown]; Haiti .. *haitensis*
3b. Epigynum otherwise, seminal receptacles straight 4
4a. Duct in palpal tegulum in ventral view with one large loop (Fig. 119); epigynum with a knob or transverse projection having an anterior extension at each end (sometimes missing) (Figs. 124, 125); widespread from Costa Rica to Paragnay ..... *attenuatus*
4b. Duct in palpal tegulum wavy and with an ectal loop in ventral view (Fig. 117); [female unknown]; Peru ..... *schlingeri*

Key to the *A. argyrodes* group species

Males

1a. A dark line or carina from lower margin of radix tip runs more or less parallel to sides of radix (Fig. 129); end of clypeal projection turned upward (Fig. 128) ..... *elevatus*
1b. Radix, clypeal process otherwise 2
2a. Line or carina from lower margin of radix tip runs at an angle to sides (Fig. 134), clypeal projection swollen at end (Fig. 133) ..... *nephilae*
2b. Radix, clypeal process otherwise 3
3a. Lateral spur of radix large and projecting from a swelling (Fig. 139); U.S.A., Mexico ..... *pluto*
3b. Lateral spur of radix small and not projecting from a swelling (Fig. 144); Peru ..... *weyrauchi*

Females

1a. Fossae of epigynum their diameter or less apart (Figs. 142, 147) 2
1b. Fossae separated by more than two diameters (Figs. 132, 137) 3
2a. Fossae bordered all around (Fig. 147); Peru ..... *weyrauchi*
2b. Fossae bordered on only three sides (Fig. 142); U.S.A., Mexico.. *pluto*
3a. Abdomen silvery; carapace length: 0.70-1.00 mm, Florida; 0.80-1.10 mm, West Indies ..... *nephilae*
3b. Abdomen sometimes silvery; carapace length: 1.05-1.40 mm, southern U.S.A.; 1.20-1.65 mm, West Indies ..... *elevatus*

Key to the *A. cordillera* group species

1a. Palpal embolus corkscrew-shaped (Fig. 161); clypeus with a projection bearing a brush of setae (Fig. 160); fossae of epigynum divided by an anteriorly directed scape (Fig. 164); Colombia ..... *rossi*
1b. Palpal embolus not corkscrew-shaped; clypeus, epigynum otherwise.. 2
2a. Distal end of palpal embolus straight (Fig. 156); epigynum with two dark openings more than their diameter apart (Fig. 159); Ecuador.. *cordillera*
2b. Epigynum with a semicircular posterior rim (Fig. 167); [male unknown]; southeastern Brazil ..... *fulvus*

Key to the *A. cancellatus* group species

Males

1a. Clypeus projecting below, projection with two lobes anterior to chelicerae (Figs. 178, 194) 2
1b. Clypeus otherwise 5
2a. Palpal radix U-shaped (Fig. 189); Panama to Ecuador ..... *atopus*
2b. Palpal radix otherwise; Ecuador, northern Peru 3
3a. Palpal radix with two prominent teeth (Fig. 179) ..... *cochleaforma*
3b. Palpal radix otherwise 4
4a. Palpal radix with a distal ventral projection bearing several small teeth (Fig. 195) ..... *proboscifer*
4b. Palpal radix with a notch (Fig. 184) ..... *sullana*
5a. A projection of clypeus surrounding deep groove (Fig. 168); southern Brazil ..... *plaumanni*
5b. Clypeus otherwise 6
6a. Tegulum in ventral view showing clearly two concentric duct loops (Figs. 207, 232) 7
6b. Tegulum in ventral view showing only one loop, or not showing duct, or loops not concentric 11
7a. Clypeus bulging and hanging below base of chelicerae (Fig. 212) ..8
7b. Clypeus not hanging below base of chelicerae (Fig. 206) 9
8a. Palpus as illustrated by Figures 218-220; Panama to Bolivia..... *amplifrons*

8b. Palpus as illustrated by Figure 213; Venezuela to Brazil .. *altus*
9a. Palpal radix with an anterior ventral thorn (Fig. 232); West Indies *exiguus*
9b. Palpal radix otherwise 10
10a. Duct diameter of inside loop twice as wide as outside loop (Fig. 207); Panama .....*gertschi*
10b. Duct diameter of two loops subequal (Fig. 226) .....*acuminatus*
11a. Radix narrow with long spine and teeth on ventral end (Fig. 174); Peru .....*woytkowskii*
11b. Radix otherwise 12
12a. Radix extended across ventral face of palpus almost touching cymbium on ectal side (Figs. 381, 386); Peru 13
12b. Radix not extended across ventral face of palpus 14
13a. Cymbium much narrower at distal end than in middle (Fig. 381) .. *peruensis*
13b. Sides of cymbium almost parallel (Fig. 386) .....*subflavus*
14a. Tegulum short, selerotized radix split into two sclerites (Fig. 200); Panama .....*arthuri*
14b. Tegulum, radix otherwise 15
15a. Radix with a long, narrow anterior spine (Fig. 409); clypeus bulging some distance below anterior median eyes (Fig. 408); southern Brazil *striatus*
15b. Radix, clypeus otherwise 16
16a. Anterior ventral edge of radix with two visible teeth in ventral view (Figs. 366, 401) 17
16b. Radix otherwise 18
17a. Spirals of embolus visible in ventral view (Fig. 366); Texas to Ecuador *subdolus*
17b. Spirals of embolus not visible in ventral view (Fig. 401); southern Brazil .....*affinis*
18a. Median apophysis in ventral view showing two almost parallel ducts (Figs. 282, 287) 19
18b. Median apophysis otherwise 20
19a. Ducts transverse to long axis of palpus (Fig. 282); clypeus bulging below eyes (Fig. 281); southern Mexico to northern Brazil *ululans*
19b. Ducts almost longitudinal (Fig. 287); clypeus not bulging below eyes (Fig. 286); Central America .....*bryantae*
20a. Eye region projecting beyond clypeus (Fig. 395); southeastern Brazil, Paraguay .....*alticeps*
20b. Eye region not projecting beyond clypeus 21
21a. Clypeus projecting at almost right angle below anterior median eyes and hanging below base of chelicerae (Fig. 370); Texas, Mexico ... *davisi*
21b. Clypeus otherwise 22
22a. In ventral view duct in tegulum looping from anterior ectal side ..23
22b. In ventral view duct in tegulum not visible or only a longitudinal portion of duct visible 33

23a. Height of clypeus below seam more than twice height above seam (Figs. 271, 276) 24
23b. Clypeal seam at about middle of carapace height 25
24a. Thread portion of embolus visible in ventral view (Fig. 277); northern Mexico ..... *taeter*
24b. Thread portion of embolus hidden by radix (Fig. 272); Florida, Mexico ..... *maculosus*
25a. Tip of radix hook widened, truncate (Fig. 338); West Indies ..... *darlingtoni*
25b. Tip of radix hook otherwise 26
26a. Origin of embolic thread in basal portion of embolus visible in ventral view (Fig. 290); Venezuela to Peru ..... *spinosus*
26b. Origin of embolic thread not visible in ventral view 27
27a. Length of radix hook less than one-fourth radix height 28
27b. Length of radix hook at least one-third radix height 29
28a. Width of embolic thread less than space between it and radix (Fig. 343); Mexico, Guatemala ..... *godmani*
28b. Width of embolic thread greater than space between it and radix (Fig. 354); U.S.A. to Paraguay ..... *dracus*
29a. Clypeus bulging below seam (Figs. 324-331) 30
29b. Clypeus straight below seam (Fig. 302) 31
30a. Clypeus bulge hanging in front of base of chelicerae (Figs. 324-331); eastern U.S.A. ..... *cancellatus*
30b. Clypeus bulge not hanging in front of chelicerae (Fig. 375); Mexico, Guatemala ..... *amates*
31a. In profile, chelicerae longer than carapace height (Figs. 301, 302); southern U.S.A. to Paraguay ..... *caudatus*
31b. In profile, chelicerae shorter than carapace height 32
32a. Length of portion of embolus visible in ventral view less than half the height of radix (Fig. 348); West Indies ..... *quasiobtusus*
32b. Length of portion of embolus visible in ventral view equals height of radix (Fig. 361); Panama ..... *chickeringi*
33a. Thread portion of palpus hidden by radix (Fig. 237) 34
33b. Part of thread portion of palpus visible in ventral view 35
34a. Thread-shaped portion of embolus behind anterior edge of radix (in palpus cleared with oil, Figs. 236, 238, 240); southeastern U.S.A. to southern Brazil ..... *americanus*
34b. Thread-shaped portion of embolus behind middle of radix (in palpus cleared with oil, Figs. 248, 250, 252); southeastern U.S.A. to Ecuador *globosus*
35a. Two spirals of thread-shaped portion of embolus visible in ventral view through transparent radix (Fig. 391); Mexico ..... *leonensis*
35b. Only portion of one spiral visible in ventral view 36
36a. Clypeal seam close to ventral margin of clypeus (Fig. 295); southeastern Brazil ..... *sicki*
36b. Clypeal seam at about middle of carapace height 37
37a. Abdomen shorter behind spinnerets than in front; Jamaica ..... *jamaicensis*

37b. Abdomen one and one-half times longer behind spinnerets than in front ..... *cubensis*

Females

1a. Epigynum a transverse groove with a posterior lightly selerotized border (Fig. 177); Peru ..... *woytkowskii*
1b. Epigynum without posterior transverse border 2
2a. Epigynum with a central longitudinal fossa in a projection (Figs. 229, 230) ..... *acuminatus*
2b. Epigynum otherwise 3
3a. Epigynum with a slender median scape posterior to a transverse anterior margin (Fig. 399); southeastern Brazil to Paraguay ..*alticeps*
3b. Epigynum otherwise 4
4a. Epigynum with scape margins forming anterior and lateral rims of fossae (Figs. 182, 336) 12
4b. Epigynum without a scape or with a projecting scape; fossae indistinct or with posterior rim (Figs. 187, 412) 5
5a. Epigynum with a median projecting scape or knobs (Fig. 187) 6
5b. Epigynum without scape or knob 10
6a. Diameter of lateral fossae larger than that of scape (Fig. 187); Ecuador, northern Peru ..... *sullana*
6b. Fossae not distinct or diameter smaller than that of scape 7
7a. Abdomen more than three times as long behind as anterior to spinnerets 8
7b. Abdomen less than twice as long behind as anterior to spinnerets . 9
8a. Epigynum with a heavily selerotized depression posterior to scape (Figs. 203-205); Panama ..... *arthuri*
8b. Epigynum with a lightly sclerotized indistinct depression posterior to scape (Figs. 210, 211); Panama ..... *gertschi*
9a. Epigynum with an acute projecting scape flanked by openings (Fig. 193); Panama to Ecuador ..... *atopus*
9b. Epigynum with a sclerotized knob bearing indistinct openings (Fig. 198); Ecuador, northern Peru ..... *proboscifer*
10a. Epigynum with two pockets anterior to sclerotized rim (Fig. 216); Venezuela to Brazil ..... *altus*
10b. Epigynum otherwise; southeastern and southern Brazil 11
11a. Loops visible through epigynal depression (Fig. 405) ..... *affinis*
11b. Loops not visible through epigynal depression (Fig. 412) ....*rigidus*
12a. Posterior border of scape wider than diameter of lateral fossae (Figs. 265, 341) 13
12b. Posterior border of scape narrower than diameter of fossae 15
13a. Posterior border of scape rounded (Fig. 341); West Indies *darlingtoni*
13b. Posterior border of scape truncate 14
14a. Ducts short (Fig. 264); Jamaica ..... *jamaicensis*
14b. Ducts longer, with loops (Fig. 284); southern Mexico to northern Brazil ..... *ululans*

15a. Scape narrow, almost as long as total width between outsides of fossae (Fig. 369); Texas to Guatemala ..... *subdolus*
15b. Scape otherwise 16
16a. Lateral margins of fossae very wide, almost reaching genital groove (Fig. 224); Panama to Paraguay ..... *amplifrons*
16b. Lateral margins otherwise 17
17a. Scape blunt, fossae on each side with a semicircular dark mark (Fig. 280); Mexico ..... *taeter*
17b. Scape otherwise, fossae without mark 18
18a. Duct of internal genitalia simple, shorter than twice the diameter of seminal receptacles (Figs. 245, 259) 19
18b. Duct of internal genitalia coiled or with sclerotized chambers; longer than twice the diameter of seminal receptacles 21
19a. Fossae almost circular; their diameter equal to width of base of scape (Fig. 247); southeastern U.S.A. to Brazil ..... *americanus*
19b. Fossae wider than long; wider than base of scape (Fig. 260) 20
20a. Abdomen higher than long without posterior dorsal tubercle (Figs. 256, 257); southeastern U.S.A. to Ecuador ..... *globosus*
20b. Abdomen longer than high, with posterior dorsal tubercle (Fig. 268); Cuba ..... *cubensis*
21a. Scape more than three times length of fossae (Figs. 172, 257, 389) 22
21b. Scape shorter than twice length of fossae 27
22a. Ducts forming spiral coils (Fig. 388); Guatemala to southern Brazil *convolutus*
22b. Duct otherwise 23
23a. Duct loosely coiled (Fig. 171); Guianas ..... *ecaudatus*
23b. Duct otherwise 24
24a. Area posterior to scape swollen (Figs. 357, 358); Mexico to Paraguay *dracus*
24b. Area posterior to scape not swollen 25
25a. Scape long, pointed (Fig. 351); duct lumen in sclerotized chambers (Fig. 350); West Indies ..... *quasiobtusus*
25b. Scape blunt; duct lumen not in sclerotized chambers 26
26a. Duct with several heavily sclerotized coils (Fig. 363); Panama ..... *chickeringi*
26b. Duct with only the most anterior coil sclerotized (Fig. 378); Mexico, Guatemala ..... *amates*
27a. Ducts wide, short, S-shaped (Fig. 234); West Indies ..... *exiguus*
27b. Ducts otherwise 28
28a. A pair of spherical sclerotized chambers between openings and seminal receptacles (Fig. 298); southeastern Brazil ..... *sicki*
28b. No spherical chambers present 29
29a. Ducts in double coil through heavily sclerotized chambers posterior to seminal receptacles (Fig. 383); Peru ..... *peruensis*
29b. Ducts otherwise 30
30a. Ducts of about equal width (Figs. 171, 373) 31
30b. Ducts much narrower near seminal receptacles than at openings (Figs. 181, 274) 33

31a. Ducts loosely coiled (Fig. 171); Guianas ..... *ecaudatus*
31b. Ducts in tight coils (Figs. 373, 393) 32
32a. Ducts double coiled (Fig. 373); Texas, Mexico ..... *davisi*
32b. Ducts with simple coil surrounding straight portion of duct (Fig. 393); Mexico ..... *leonensis*
33a. Length of ducts only slightly more than two diameters of seminal receptacles (Fig. 181); Ecuador, northern Peru ..... *coehleaforma*
33b. Length of duct more than three diameters of seminal receptacles ... 34
34a. Ducts leaving seminal receptacles in a posterior direction (Fig. 274); Florida, Mexico ..... *maculosus*
34b. Ducts leaving seminal receptacles in a lateral or anterior direction (Figs. 293, 345) 35
35a. Duct with a loop on each side of seminal receptacle, then continuing S-shaped to opening (Fig. 293); Jamaica ..... *gapensis*
35b. Duct otherwise 36
36a. Duct with only one loop as in Figure 345; Guatemala ..... *godmani*
36b. Ducts with several loops 37
37a. Area posterior to scape swollen (Fig. 336); ducts fused and sclerotized (Figs. 333-334); eastern U.S.A. ..... *cancellatus*
37b. Area posterior to scape not swollen (Fig. 320); ducts not fused Figs. 311-318); southern U.S.A. to Paraguay ..... *caudatus*

The *Rhomphaea* group

Argyrodes fictilium (Hentz)

Figures 6, 7, 26-28; Map 1

Theridion ? fictilium Hentz, 1850, Jour. Boston Soc. Nat. Hist., vol. 6, p. 282, pl. 10, fig. 4; 1875, Occ. Papers Boston Soc. Nat. Hist., vol. 2, p. 155, pl. 17, fig. 4 [query Hentz's]. Female type from Alabama, lost.

Argyrodes fictilium, Emerton, 1882, Trans. Connecticut Acad. Arts and Sci., vol. 6, p. 24, figs. 2, 2a.

Rhomphaea remota Bryant, 1940, Bull. Mus. Comp. Zool., vol. 86, p. 308, fig. 74. Male holotype from Trinidad Mts., Cuba, in the Museum of Comparative Zoology, examined by Levi. NEW SYNONYMY.

Rhomphaea fictilium, Kaston, 1948, Bull. Connecticut Geol. Nat. Hist. Surv., no. 70, p. 89, figs. 85, 86. Bonnet, 1958, Bibliographia Araneorum, vol. 2, pt. 4, p. 3864.

Rhomphaea lacerta, Chamberlin and Ivie, 1944, Bull. Univ. Utah, biol. ser., vol. 8, no. 5, p. 45, fig. 54. Archer, 1946, Paper Alabama Mus. Nat. Hist., no. 22, p. 25. Probably not *Tetragnatha lacerta* Walckenaer, 1841.

Note. The specific name is used as a noun in apposition.

Description. Male from Missouri. Carapace, legs, sternum, and palpi pale yellow, with parallel brown stripes from anterior median eyes to anterior margin of clypeus, and some brown on thorax. Abdomen tan with silvery spots, and some brownish

streaks on sides. Eyes on single tubercle, those of each side almost touching, and widely separated from those of other side, with anterior medians and posterior medians about equal in size, larger than lateral eyes. Clypeus slanting, long (Fig. 7). Legs and palpi very long, slender. Abdomen very long, worm-like; covered, at least in posterior part, with long, fine hairs; tip usually pointed but without cuticular spine. Total length 5.0 mm. Carapace 1.8 mm long. First femur, 6.4 mm; patella and tibia, 5.4 mm; metatarsus, 3.4 mm; tarsus, 1.7 mm.

Female from Missouri. Color similar to that of male; a reddish brown stripe on palpi; patella and distal part of metatarsus of first leg brown. Abdomen darker than in male, pale brown dorsally and on sides covered with silvery flecks. Clypeus and eyes as in male. Chelicerae with one tooth on anterior, one on posterior margin. Abdomen much heavier than that of male and tapering evenly to tip (Fig. 26). Total length 10.5 mm, with posterior part of abdomen sinuous and tip curled upward. Carapace 1.5 mm long. First femur, 7.3 mm; patella and tibia, 5.7 mm; metatarsus, 3.2 mm; tarsus, 1.6 mm.

Variation. The abdomen varies in shape as is illustrated by Figure 26. The total length varies in part with the length of the abdomen, which is often coiled either upward or downward at the posterior tip. Males measure from 3.0 to 6.6 mm, with the carapace varying from 1.0 to 1.4 mm long. Females measure from 5.6 to 12.0 mm, with carapace from 1.3 to 1.7 mm long. The color is usually pale, but a few specimens have reddish brown median stripes on the venter of the abdomen and sternum, light brown bands on carapace and the abdomen is conspicuously brownish on sides. Parts of the male palpi are more definitely sclerotized in some specimens than in others, and the embolus and conductor, which are nearly parallel in some specimens, are at a slight angle in others. The palpal tibiae are shorter in California specimens than in eastern ones. The seminal receptacles in some female genitalia appear quite far apart; those examined from the dorsal side show the receptacles separated by less than a radius. The epigynum of a female from Oregon appears slightly aberrant. The epigyna are often covered after mating by an easily removable exudation.

Diagnosis. The abdomen of *A. fictilium* is unusually long, sinuous, and evenly tapered, and lacks a spine at the tip (Fig. 26). Both embolus and conductor of the male palpus are obliquely placed in the apical half of the bulb (Fig. 6). The palpus is very long and slender, and the tarsus only slightly wider than the

distal part of the tibia. The male lacks a cephalic projection (Fig. 7) which separates it from other males described from America. The epigynum of the female has a central depression on a raised area, bordered by a sclerotized edge. The edge hides the well-separated openings of the tubes (Fig. 28). The seminal receptacles are oval and variably separated, usually by less than a radius (Fig. 28). The membranous tubes lie ventral to posterior edge of receptacles, and are invisible in dorsal view (Fig. 27).

Ecology. These spiders often make small theridiid webs of their own, but females are sometimes collected in webs of other spiders.

Distribution. From southern Canada to Panama. Widely scattered, but rare; Map 1.

Records. Canada. Ontario. Nipissing Co.: Lake Timagami, ♀ (W. J. Gertsch, W. Ivie, T. Kurata). *British Columbia.* Pender Harbour (W. Watkins); Wellington (R. Guppy); Nanaimo (R. B. Conway).

United States. Maine. Cumberland Co.: Long Island (J. H. Emerton). Hancock Co.: Mt. Desert Isl. (W. Procter). Waldo Co.: Winterport. *Massachusetts.* Barnstable Co.: Woods Hole (H. Britcher). Essex Co.: Bartholomew's Pond, Peabody (J. H. Emerton); Essex (J. H. Emerton). Middlesex Co.: Lexington (J. H. Emerton); Holliston (N. Banks). *Connecticut.* Norwalk, juv. (W. J. Gertsch). *New York.* Nassau Co.: Sea Cliff (N. Banks). Sullivan Co.: White Lake, juv. (H. Britcher). *Tennessee.* Robertson Co.: 30 mi. N of Nashville (W. J. Gertsch). *North Carolina.* Carteret Co.: Beaufort (R. D. Barnes). Durham Co.: Duke Forest (A. M. Chickering). Orange Co.: Chapel Hill (J. H. Emerton). Pasquotank Co.: Elizabeth City (J. H. Emerton). *Georgia.* Cobb Co.: Marietta (J. H. Emerton). Ware Co.: Waycross (W. J. Gertsch). (Chamberlin and Ivie, 1944). *Florida.* Alachua Co.: W of Gainesville (W. J. Gertsch). Hillsborough Co.: Hillsborough River State Park (W. J. Gertsch). Lake Co.: Leesburg (M. Statham). Liberty Co. (H. K. Wallace). Okeechobee Co.: Okeechobee (W. J. Gertsch). *Alabama.* (Archer, 1946). *Mississippi.* Amite Co.: Gloster (A. F. Archer). Forrest Co.: Hattiesburg (A. F. Archer). *Missouri.* Madison Co.: 14 mi. E of Farmington (H. E., D. L. Frizzell). Phelps Co.: near Rolla (H. E., D. L. Frizzell). *Texas.* Denton Co.: Dallas (S. Jones). Travis Co.: Austin (H. E., D. L. Frizzell). *Washington.* King Co.: Seattle (M. H. Hatch). San Juan Co.: Friday Harbor (M. H. Hatch). *Oregon.* Coos Co.: Camp Myrtlewood, 1½ mi.

S of Bridge (V. Roth). Yamhill Co.: McMinnville (K. M. Fender). *California.* Marin Co.: Mill Valley (W. J. Gertsch, V. Roth). Monterey Co.: Pacific Grove, juv. (J. C. Bradley); Big Sur, juv. (W. J. Gertsch). Santa Clara Co.: Palo Alto (A. M. Nadler); near Stanford Univ. (L. W. Swan). Santa Cruz Co.: Big Basin, juv. (R. X. Schick).

Mexico. Nuevo León: El Papalote, km 1120 (A. F. Archer). *Panama Canal Zone.* Summit; Barro Colorado Isl.; Experimental Gardens; Forest Reserve (all A. M. Chickering). *Cuba.* (Bryant, 1940). *Jamaica.* St. Andrew's Par.: Mona, ♂ (A. M. Chickering). Trelawny Par.: Falmouth (C., P. Vaurie). *Puerto Rico.* Luquillo Mts., ♀ (H. Beatty). *Paraguay.* Territ. Fonciere, June 3, 1908, ♀ (E. Reimoser coll.) [erroneous locality?].

Argyrodes projiciens (O.P.-Cambridge), new combination

Figures 8-10, 29-31; Map 2

Rhomphaea projiciens O.P.-Cambridge, 1896, Biologia Centrali-Americana, Araneidea, vol. 1, p. 186, pl. 23, figs. 9, 10. Male, female syntypes from Teapa, Tabasco, Mexico, in the British Museum (Natural History), examined by Levi. F.P.-Cambridge, 1902, *op. cit.*, vol. 2, p. 407, pl. 38, figs. 17, 18.

Rhomphaea spinosa Badcock, 1932, Jour. Linnean Soc. London, vol. 38, p. 8. Immature female from Paraguay, in the British Museum (Natural History), examined by Levi. NEW SYNONYMY.

Rhomphaea martinae Exline, 1950, Studies Honoring Trevor Kincaid, Univ. of Washington Press, p. 116, figs. 5, 7, 8, 14, 16. Male holotype from Chira River Valley, Piura, Peru, in the Museum of Comparative Zoology. NEW SYNONYMY.

Note. Specimens from Cuba, identified as *R. projiciens* by Franganillo, have the tip of the abdomen divided; they are probably *Argyrodes furcatus.* Only female specimens have been found in the United States, Mexico, Brazil and Paraguay.

Description. Male from Panama Canal Zone. Carapace pale yellow, thoracic part with irregular gray band on each side and on clypeus from anterior median eye to edge, sometimes continuing on face of chelicerae. Legs and palpi pale, irregularly annulated with light brown, and streaked with reddish longitudinal lines and spots. Sternum pale with irregular brownish lateral bands uniting behind and almost uniting anteriorly. Abdomen pale with brownish streaks on venter and around spinnerets, large dark gray patches on posterior part of abdomen, which is thickly covered with irregular silvery spots. Carapace low with eyes and cephalic projection on low tubercle. Eyes small, anterior

median eyes a little larger than others, contiguous with anterior lateral eyes. Posterior median eyes separated by about a diameter and close to posterior lateral eyes. Cephalic projection arising from between anterior median eyes, slender proximally, gradually thickened distally with a ventral tip bearing a brush of curved setae (Figs. 9, 10). Clypeus straight, slanting a little forward, a little higher than length of chelicerae. Legs long, thin, thickly covered with hair-like setae. Abdomen slender, projecting dorsally from spinnerets. Posterior tip wrinkled, bluntly rounded with a long sclerotized spine. Total length 3.2 mm. Carapace 1.5 mm long with cephalic projection, 1.2 mm without. Abdomen 2.9 mm long. First femur, 4.7 mm; patella and tibia, 4.5 mm; metatarsus, 2.5 mm; tarsus, 1.3 mm.

Female from same locality. Color as in male but brighter, brownish bands uneven and forming a reticulated pattern. Carapace somewhat raised behind thoracic groove, and eye tubercle more prominent than in male. Chelicerae with one quite prominent tooth on upper margin of furrow, two to three smaller ones on lower. Clypeus a little more slanting than in male. Posterior median eyes a little farther apart. Abdomen extending far above spinnerets; tip as in male with the long spine (Fig. 29). Total length 4.0 mm. Carapace 1.5 mm long. Abdomen 6.6 mm long. First femur, 5.6 mm; patella and tibia, 4.7 mm; metatarsus, 2.8 mm; tarsus, 1.4 mm.

Figures 30, 31 were prepared from the type of *Rhomphaea projiciens*.

Variation. Males are from 3.0 to 5.0 mm long, depending mostly on direction of the posterior portion of the abdomen, which is sometimes at right angles to carapace, sometimes almost straight. Some males are pale yellow with faint markings and silvery abdomens. Others have conspicuous markings of red and brown on carapace and legs, and abdomen with blackish patches with only a few silvery spots. Color, length and direction of the abdomen even more variable in females (from Panama, Brazil and Paraguay). Dark specimens may have a light brown carapace with blackish bands, legs and palpi orange with black and red markings, and abdomen mostly reddish brown with black patches and only a thin silvery reticulation. Length varies from 3.0 to 6.5 mm. The caudal spine is usually present, but may be short, bent over, broken, or sometimes missing.

Diagnosis. The shape of the cephalic projection (Figs. 9, 10) separates males from *A. procerus* and *A. metaltissimus* with which they have been confused. The long and slender palpus has

radix, conductor and embolus all drawn out, slender (Fig. 8), and directed almost parallel to the long axis of the tarsus. This species is lightly colored; dark females in Panama are usually either *A. projiciens* or *A. paradoxus*. *Argyrodes projiciens* can be separated by the epigynum (Fig. 31) which is slightly swollen, not reaching the genital groove. Posterior to a shallow longitudinal median groove lie two small, indistinct, somewhat distant openings. There is no sclerotized edge behind openings as in *A. procerus*. The shallow groove may be difficult to see because of scattered pigment. The openings are somewhat variable in appearance due to the amount of sclerotization at the ends of the tubes. The connecting tubes are simple and weakly sclerotized (Fig. 30).

Distribution. Florida, Texas to Paraguay. None have been identified from the West Indies; Map 2.

Records. United States. Florida. Dade Co.: Royal Palm Park, Everglades Natl. Park, ♀ (W. S. Blatchley). *Texas.* Hidalgo Co.: San Juan. Travis Co.: Austin (A. Flury); near Austin (D. L., H. E. Frizzell).

Mexico. Oaxaca: Playa Hati (H. Wagner). *Chiapas:* Finca Cuauhtemoc, near Cacahoatán (C., M. Goodnight); Puerto Madero (C., M. Goodnight). *Guatemala.* San Jerónimo (C., P. Vaurie). *Panama.* Arraiján; Boquete; El Valle (all A. M. Chickering). *Panama Canal Zone.* Barro Colorado Isl.; Experimental Gardens; Chilibre; Madden Dam; Summit (all A. M. Chickering); Barro Colorado Isl. (A. M. Nadler).

Ecuador. Guayas: Milagro. *Peru. Piura:* Pariñas Valley; Chira River Valley. *Brazil. Bahia:* Condeúba (E. Gounelle, MNHN). *Minas Gerais:* Caraça (E. Gounelle, MNHN). *Rio de Janeiro:* Rio de Janeiro (Germain, MNHN). *Santa Catarina:* Nova Teutonia, lat 27°11′, long 52°23′ (F. Plaumann, SMF). *Paraguay.* (MNHN). *Alto Parana:* Apa; Taguararapa.

Argyrodes procerus (O.P.-Cambridge), new combination

Figures 11-13, 32-34; Map 2

Rhomphaea sp. Simon, 1894, Histoire Naturelle des Araignées, vol. 1, fig. 507. Female from Venezuela.

Ariamnes procera O.P.-Cambridge, 1898, Biologia Centrali-Americana, Araneidea, vol. 1, p. 257, pl. 38, fig. 5. Female type from Bugaba, Panama, in the British Museum (Natural History), examined by Levi.

Rhomphaea procera, F.P.-Cambridge 1902, Biologia Centrali-Americana, Araneidea, vol. 2, p. 407, pl. 38, fig. 19.

Rhomphaea simoni Petrunkevitch, 1911, Bull. Connecticut Acad. Sci., vol. 29, p. 186. Name for *Rhomphaea* sp. Simon, 1894, *op. cit.*, fig. 507. NEW SYNONYMY.

Note. A female specimen in the Muséum National d'Histoire Naturelle, Paris, from San Estebán, Venezuela, collected by Simon, has the long abdomen rounded at the tip, as in Simon's (1894) illustration, named by Petrunkevitch.

Description. Male from Panama Canal Zone. Carapace pale yellow with a few irregular grayish markings on thorax, and a pair of pale gray, longitudinal bands on clypeus. Legs nearly white with a few pale gray spots. Sternum with a pair of longitudinal gray bands united posteriorly. Integument of abdomen yellowish, almost entirely covered with silver; a few gray spots near tip and a grayish band from spinnerets to tip. Carapace low with raised eye tubercle. Median eyes widely separated. Anterior median eyes largest, lateral eyes smallest and somewhat irregular in shape. Cephalic projection arises from median ocular area, and is expanded distally into a fleshy knob, without conspicuous long setae (Figs. 12, 13). Clypeus as high as chelicerae are long, projecting below. Abdomen very slender and tapering evenly behind spinnerets. Tip pointed but without spine. Total length 3.9 mm. Carapace 1.1 mm long. First femur, 5.4 mm; patella and tibia, 5.0 mm; metatarsus, 2.5 mm; tarsus, 1.2 mm.

Female from Panama Canal Zone. Carapace color as in male, with palpal segments gray ventrally. Sternum yellow with gray in middle spreading to sides in a reticulated pattern. Legs very pale with a few dark spots. Abdomen pale yellow covered with silver as in male but with more gray markings on sides and underneath, and a few dark, widely scattered spots. Carapace raised behind thoracic groove and at eye tubercle. Eyes as in male. Clypeus more rounded and slanting than in male. Abdomen similarly tapered and elongate behind spinnerets, but larger and thicker than in male, with a small membranous spine at tip (Fig. 32). Total length 6.4 mm. Carapace 1.5 mm long. First femur, 7.3 mm; patella and tibia, 6.4 mm; metatarsus, 2.6 mm; tarsus, 1.4 mm. Females vary from 5.5 to 10.2 mm long, depending mostly on length of abdominal projection.

Figures 33, 34 were prepared from the type of *Ariamnes procera.*

Diagnosis. Argyrodes procerus is paler and more fragile than other species in Panama, and is without spine on abdomen. The male differs from *A. projiciens* by smaller size, carapace shape

and a differently shaped projection (Figs. 12, 13). The palpus is similar to that of *A. projiciens* but has a wider tegulum, a shorter embolus and a longer, thinner, nearly rectangular radix (Fig. 11). The unique epigynum is very lightly sclerotized, flat with a pair of small, contiguous openings near the posterior edge, sometimes separated. The openings are anterior to diagnostic, though faint, sclerotized margin (Fig. 34). The margin may be straight, wavy or curved. The seminal receptacles are comparatively small, broadly oval, separated but not far apart. The tubes are simple and narrow, extending from the openings laterally to enter the receptacles on the posterior margin (Fig. 33). (Males and females have not been taken together, and have been matched on the basis of color and position of the eyes.)

Distribution. Costa Rica to Venezuela; Map 2.

Records. Costa Rica. Cartago, Nov. 1953, ♀ (N. L. H. Krauss); Orosi, Oct. 1953, ♀ (N. L. H. Krauss). *Panama.* Arraiján. *Panama Canal Zone.* Experimental Gardens; Forest Reserve; Fort Sherman; France Field; Madden Dam; Balboa; Barro Colorado Isl. (all A. M. Chickering). *Venezuela. Carabobo:* San Estebán, 1888, ♀ ♂ (E. Simon, MNHN).

Argyrodes honestus new species

Figures 14, 15, 41-43; Map 2

Type. Male from Nova Teutonia, lat 27°11′ W, long 52°23′ S, Santa Catarina, Brazil (F. Plaumann), in the Senckenberg Museum, Frankfurt. The specific name is a Latin adjective meaning well-favored.

Description. Male type. Carapace very pale with only a trace of dark longitudinal bands. Cephalic projection light brown. Bands present on clypeus. Legs pale yellow with light brown annulations. Sternum pale with a pair of irregular brown stripes. Abdomen yellow with brown stripes and streaks on venter, sides, and a few on dorsum. Silver patches on dorsum. Posterior part thickly covered with silver over a tan background. Carapace flat. Anterior median eyes slightly larger than posterior median eyes. Posterior eyes separated by a diameter. Cephalic projection arises from area between median eyes, more slender than that of *A. metaltissimus*, slightly constricted near base; distal part with a ventral tip bearing a tuft of forward pointing setae (Fig. 15). Clypeus high, straight, with considerable space between edge of clypeus and base of chelicerae. Abdomen very slender, greatly prolonged behind and above spinnerets,

terminating in a membranous point. Non-lanceolate setae on posterior part short and lying against abdomen. Total length 4.0 mm. Carapace 1.3 mm long, with cephalic projection; 1.1 mm long without. First femur, 4.5 mm (other segments missing).

Female paratype. Color as in male; abdomen almost entirely silver with a few dark markings toward tip. Carapace as in male with eye region raised and tuberculate. Clypeus straight, slanting a little forward, not as high as chelicerae are long. Abdomen very high, seemingly with a circlet of long, prone, roughened setae. Posterior tip missing. Total length 4.5 mm. Carapace 1.5 mm long. First femur, 6.2 mm (other segments missing).

Variation. A male from Venezuela is nearly identical to type specimen but the ventral tip on the cephalic projection is larger.

Diagnosis. Argyrodes honestus is less well-marked than related species and the tip of the abdomen is more pointed (Fig. 41). Male cephalic projection (Fig. 15) is more slender than that of *A. metaltissimus*. Palpi have the tarsi narrower and longer. Palpal sclerites are similar to those of *A. metaltissimus,* except that radix is short and has sides nearly parallel without distal hook (Fig. 14). Epigynum flatter than in *A. metaltissimus*. Posterior depression inconspicuous. Fossa wider than long (Fig. 43), showing paired tube openings on posterior margin when abdomen is tilted. Tubes narrow, sclerotized, passing posterior rather than lateral, then folding dorsally to form a straight transverse line and bending ventrally to seminal receptacles. Seminal receptacles small, broadly oval, less than a diameter apart (Fig. 42).

Distribution. Venezuela to southern Brazil; Map 2.

Records. Venezuela. ♂ (SMF). *Brazil. Santa Catarina:* Nova Teutonia, ♀ paratype (F. Plaumann, SMF).

Argyrodes metaltissimus (Soares and Camargo), new combination

Figures 16-22, 35-40; Map 2

Rhomphaca metaltissima Soares and Camargo, 1948, Bol. Mus. Paraense, vol. 10, p. 365, figs. 15-18. Male holotype from Chavantina, Mato Grosso, Brazil, in the Departamento de Zoologia da Secretaria da Agricultura, São Paulo, examined by Levi.

Description. Male from Panama Canal Zone. Carapace yellow with a dark gray longitudinal band near each lateral margin, and a pair of bands on clypeus. Legs pale yellow, inconspicuously annulate with light brown. Sternum pale with a pair of longitudinal bands uniting posteriorly. Abdomen very pale with a

dark gray ventral band, large black streaks and irregular spots, especially toward posterior tip and between spinnerets and tip. Silvery patches scattered over dorsum and posterior part. Carapace unusually flat. Anterior median eyes much larger than others and overhanging clypeus. Eyes of each side nearly contiguous. Posterior median eyes separated by a little more than their diameter. Lateral eyes smaller than others. Cephalic projection arising between anterior median eyes, large and fleshy, slightly irregular in outline, with entire tip setae-bearing but setae not forming a brush or tuft (Figs. 17-22). Clypeus slightly concave, not quite as high as chelicerae are long. Legs very long and densely clothed with fine setae. Abdomen slender from base to spinnerets, somewhat bulging at level of spinnerets and tapering to blunt tip. Tip with integument wrinkled, bearing scattered, long, black, flattened lanceolate setae (often missing from alcoholic specimens, though scars remain). Posterior part of living abdomen probably movable in a worm-like fashion; some preserved specimens have abdomen sinuous or curled upward or downward. Total length 4.0 mm. Carapace 1.5 mm long, with cephalic projection, 1.2 mm without. First femur, 5.5 mm; patella and tibia, 4.8 mm; metatarsus, 3.0 mm; tarsus, 1.6 mm.

Female from same locality. Color as in male except that palpi have a dark gray ventral line. Carapace, eyes, clypeus and legs as in male. Abdomen not so slender as in male and usually longer with tip blunt and setae as in male. Shape of posterior part variable as in male. Total length 4.3 mm. Carapace 1.3 mm long. First femur, 7.0 mm; patella and tibia, 6.0 mm; metatarsus, 3.8 mm; tarsus, 2.0 mm.

Figure 17 was prepared from the type, Figures 36-38 from a paratype.

Variation. There seems to be considerable geographic variation of the male carapace projection (Figs. 17-22). The male type and female paratype show significant differences from Panamanian specimens. The carapace projection of the type is heavier (Fig. 17). Unfortunately the carapace of the type is badly damaged and palpi are missing. The connecting ducts of the female paratype are considerably wider and more heavily sclerotized near the opening (Fig. 37). The abdomen of the female paratype is longer (Fig. 36) than in specimens from Panama (Fig. 35).

Diagnosis. The shape of the cephalic projection of the male (Figs. 17-22) is diagnostic. The genital structures are similar to those of *A. honestus*. The embolus is U-shaped. The radix is

flat, elongate, one edge entire, the inner margin expanded medially, then contracting to form a broad hook distally which, unlike the hook of related species, has only few teeth. Conductor long, membranous, leaf-like, with distal end approaching tip of embolus (Fig. 16). The palpus of *A. metaltissimus* differs from that of *A. honestus* in having a shorter, straighter embolic tube, and a wider space between tube and basal part. The epigynum is lightly sclerotized (Figs. 38, 40). The tubes extend some distance laterally (Figs. 37, 39) while in *A. honestus* the tubes extend posteriorly and are parallel. The tubes are somewhat sclerotized, often diminishing in size toward receptacles (Figs. 37, 39).

Distribution. Panama, Venezuela to central Brazil; Map 2.

Records. Panama Canal Zone: Barro Colorado Isl., ♀ ♂ (N. Banks; A. M. Chickering). *Lesser Antilles. Trinidad:* Simla near Arima, Dec. 29-30, 1954, ♀ ♂ ; Feb. 28, 1959, ♂ (A. M. Nadler). *Venezuela. Aragua:* Rancho Grande, Dec. 20, 1954, ♂ (A. M. Nadler). *Brazil. Mato Grosso:* Chavantina, ♀ paratype.

Argyrodes paradoxus Taczanowski

Figures 23-25, 44-50; Map 2

Argyrodes paradoxa Taczanowski, 1872 (1873), Horae Soc. Ent. Rossicae, vol. 9, p. 121, pl. 5, fig. 13. Female type from Cayenne, French Guiana, in the Polish Academy of Sciences, Warsaw, examined by Levi.

Ariamnes spinicaudatus Keyserling, 1884, Die Spinnen Amerikas, Theridiidae, pt. 1, p. 171, pl. 8, fig. 104. Immature male here designated lectotype from Amable María [dept. Junín, prov. Tarma], Peru, in the Polish Academy of Sciences, Warsaw, examined by Levi. NEW SYNONYMY.

Rhomphaea petrunkevitchi Mello-Leitão, 1945, Trans. Connecticut Acad. Sci., vol. 36, p. 171, fig. 1. Male type from Jaraguá, Goiás, Brazil, in the Museu Nacional, Rio de Janeiro, not available for examination. NEW SYNONYMY.

Note. Identification of Panamanian material with *Ariamnes spinicaudatus* is based on unusually long, curved embolus, as seen through palpal cuticle of immature lectotype (Fig. 25).

Description. Male from Panama Canal Zone. Carapace bright yellow with a dark gray band on each lateral margin posteriorly, and a gray band from anterior median eyes to tip of chelicerae. Cephalic projection a little darker than rest of carapace. Palpi with ventral, dark gray stripe. Sternum yellow with a pair of wide gray bands joining anteriorly and posteriorly. Legs yellow with irregular light brown annulations. Abdomen yellow with large grayish patches thickly interspersed with silvery spots.

Clypeus high and steep, nearly as high as chelicerae are long. Eyes on common tubercle, those of each side close together. Median eyes widely separated, anterior medians largest. Long, stout cephalic projection arising from median ocular area ending in a blunt dorsal tip and a longer setae-bearing, ventral tip (Fig. 24). Chelicerae weak, armed with a long tooth on anterior margin of fang groove, two small teeth on posterior margin. Abdomen slender, extending beyond spinnerets, ending in a short, stiff spine. Total length including cephalic projection, 5.5 mm. Carapace 1.6 mm long with, 1.1 mm without projection. First femur, 4.8 mm; patella and tibia, 4.6 mm; metatarsus, 2.6 mm; tarsus, 1.3 mm.

Female from same locality. Cephalothorax as in male but pattern reddish brown rather than gray, with additional streaks on carapace and legs, anterior tibiae entirely reddish brown underneath. Abdomen as in male but darker, and silvery flecks evenly and thickly distributed over integument. Carapace, eyes, chelicerae as in male but without projection. Abdomen larger, heavier, shaped approximately as in male and with a short spine at posterior tip (Fig. 44). Total length 5.2 mm. Carapace 1.5 mm long. First femur, 7.0 mm; patella and tibia, 6.0 mm; metatarsus, 3.4 mm; tarsus, 1.6 mm.

Figures 45 and 46 were prepared from the type of *A. paradoxus;* Figure 25 from the type of *Ariamnes spinicaudatus.*

Variation. The epigynum (Figs. 46, 49) is quite variable and the ducts vary in length (Figs. 45, 48). Unfortunately too few males were available to study variation.

Diagnosis. This species is often darker than others of the *Rhomphaea* group. The size and shape of the cephalic projection (Fig. 24) separate males from other species. Unlike related species, the embolus is long and hook-shaped. The conductor is long, membranous; the radix is long, slender, somewhat curved at tip (Fig. 23). The epigynum is diagnostic, having a posterior depression, bordered by a variable ridge anteriorly, in front of which is a pair of large, sometimes indistinct, openings (Figs. 46, 49). The seminal receptacles are large, oval, almost touching. The long tubes form a pair of lateral loops on each side (Figs. 45, 48).

Distribution. Mexico, Peru to Minas Gerais; Map 2.

Records. Mexico. Veracruz: 16 km S of San José del Carmen, April 16, 1953, ♀ (L. I. Davis). *Panama.* El Volcán, Chiriquí, Feb. 19, 1936, ♀ (W. J. Gertsch); Cerro Punta, Chiriquí, March 4, 1936, ♀ (W. J. Gertsch). *Panama Canal Zone:* Barro Colorado Isl., July 1936, ♀; Aug. 1936, ♀; June 1939, ♀; Aug.

1950, ♀; July 1954, ♂; Aug. 14, 1954, ♀ ♂; Summit, July 1950, ♂; Experimental Gardens (all A. M. Chickering). *Venezulea. ? Dist. Fed.:* Hacienda Corosal near Mt. La Silla, 1888, ♀ (E. Simon, MNHN). *Brazil. Minas Gerais:* Caraça (E. Gounelle, MNHN).

The *A. trigonum* species group

Argyrodes obscurus Keyserling

Figures 79-83; Map 3

Argyrodes montanus Keyserling, 1884, Die Spinnen Amerikas, Theridiidae, pt. 1, p. 193, pl. 9, fig. 115. Female type from Montana di Nancho, [? Cajamarca], 8000′ elev. [2550 m], Peru, in the Polish Academy of Sciences, Warsaw, examined by Levi.

Argyrodes obscurus Keyserling, 1884, *op. cit.*, p. 194, pl. 9, fig. 116. Male from Montana di Nancho, [? Cajamarca], 8000′ elev. [2550 m], Peru, in the Polish Academy of Sciences, Warsaw, examined by Levi. NEW SYNONYMY.

Note. The name of the male type is chosen as the name of the species, because males are easier to determine.

Description. Female from Huánuco, Peru. Carapace orange-brown, legs a little paler. Sternum reddish brown. Dorsum of abdomen pale gray anteriorly, nearly black posteriorly; sides and venter dark reddish gray becoming red toward tip of abdomen. Eyes small, nearly equal in size. Anterior medians separated by two diameters; area occupied by median eyes forming a square. Clypeus high, steep, with a deep furrow under eyes (Fig. 79). Abdomen extending beyond spinnerets, with conspicuously bifurcated tip. Total length 3.8 mm. Carapace 1.4 mm long. First femur, 2.8 mm; patella and tibia, 2.4 mm; metatarsus, 1.5 mm.

Figures 79 and 80 were prepared from the type of *A. obscurus;* Figures 81-83 from the type of *A. montanus.*

Diagnosis. The cephalic process of the male is more blunt and the clypeal process shorter (Fig. 79) than in other South American species. The process differs in shape from that of *A. concisus.* The embolus of the palpus is short and narrow. The radix is long with parallel sides (Fig. 80). The eyes are smaller than in related species. The anterior median eyes of the female are unusually widely separated. The median ridge of the epigynum is long and wide and becomes wider anteriorly with a small anterior depression (Fig. 83). The openings are nearly invisible. The seminal receptacles are separated by little more than a radius (Fig. 82).

Records. Peru. Huánuco: Monzón Valley, near Tingo María, Oct. 15, 1954, ♀ (E. I. Schlinger, E. S. Ross).

Argyrodes furcatus (O.P.-Cambridge)

Figures 84-88; Map 3

Ariamnes furcata O.P.-Cambridge, 1898, Biologia Centrali-Americana, Araneidea, vol. 1, p. 129, pl. 17, fig. 10. Female type from Teapa, Tabasco [Mexico], in the British Museum (Natural History), examined by Levi.

Argyrodes furcata O.P.-Cambridge, 1898, *op. cit.*, p. 258, pl. 38, fig. 3. Female type from Omilteme, Guerrero, 9500 ft. [2900 m, Mexico], in the British Museum (Natural History), examined by Levi. NEW SYNONYMY.

Argyrodes trigonus, F.P.-Cambridge, 1902, Biologia Centrali-Americana, Araneidea, vol. 2, p. 404, pl. 38, figs. 7, 8. Not *A. trigonum* (Hentz).

Rhomphaea furcata, F.P.-Cambridge, 1902, *op. cit.*, vol. 2, p. 407, pl. 38, fig. 15. For *Ariamnes furcata* O.P.-Cambridge.

Rhomphaea bifissa F.P.-Cambridge, 1902, *op. cit.*, p. 407, pl. 38, fig. 16. New name for *Argyrodes furcata* O.P.-Cambridge, preoccupied by *Ariamnes furcata* O.P.-Cambridge. Kraus, 1955, Abhandl. Senckenbergischen Naturf. Gesell., vol. 493, p. 16. NEW SYNONYMY.

Argyrodes frontatus Banks, 1908, Canadian Ent., vol. 40, p. 208, fig. 9, upper right. Syntypes from Ocean Springs, [Jackson Co.], Mississippi, in the Museum of Comparative Zoology, examined by Levi. NEW SYNONYMY.

Conopistha trigonum, Bryant, 1940, Bull. Mus. Comp. Zool., vol. 86, p. 308. Not *A. trigonum* (Hentz).

Conopistha rufa, Chamberlin and Ivie, 1944, Bull. Univ. Utah, biol. ser., vol. 8, no. 5, p. 38. Probably not *Linyphia rufa* Walckenaer.

Note. Linyphia rufa Walckenaer, 1841 (Histoire Naturelle des Insectes Aptères, vol. 2, p. 284) was resurrected by Chamberlin and Ivie, 1944, as an older name for *A. trigonum* (Hentz), based on a series of specimens collected in Georgia, which, however, belong to *A. furcatus.* Both species, *A. furcatus* and *A. trigonum,* are found in Georgia, although the former is far more common. No diagnostic characters are mentioned by Walckenaer, nor reproduced in Abbot's drawings. Since *L. rufa* has seldom been used for *trigonum* and never for *furcatus,* it seems best to consider it a doubtful name.

Description. Male from Mississippi. Color varies from pale whitish to dark gray or dusky black sclerotized parts. Abdomen silvery white with pale gray to black on light background. Area over lungs pale yellow. Carapace with a short cone-shaped head process, and a short clypeal process, which is blunt and at an

angle to clypeus (Fig. 84). Eyes medium sized. Posterior medians more than two diameters apart, and more than a radius from laterals. Abdomen sometimes long, with tip sometimes blunt, but usually bifurcate. Total length 2.7 mm. Carapace 1.2 mm long. First femur, 2.3 mm; patella and tibia, 1.8 mm; metatarsus, 1.4 mm; tarsus, 0.7 mm.

Female from Mississippi. Color as in male. Abdomen, however, has dark lanceolate mark on dorsum. Anterior median eyes about a diameter and a half apart. Posterior median eyes almost three diameters apart, nearly a diameter from laterals. Clypeus high. Abdomen as in male, but larger (Fig. 86). Total length 3.7 mm. Carapace 1.1 mm long. First femur, 2.6 mm; patella and tibia, 2.1 mm; metatarsus, 1.4 mm; tarsus, 0.8 mm.

Figures 86-88 were prepared from the type of *Ariamnes furcatus*.

Variation. Color variation is very marked in this species and may vary with the amount of sunshine to which the spider has been exposed. Light specimens are often found in sunny situations, dark specimens in shade. Specimens from the same area may vary from very pale gray to nearly black. A few have a reddish cast, especially on sternum and venter of abdomen. In female, shape and size of abdomen depend on stage of egg development. In large populations, individuals tend to be smaller than in small populations. Males vary from 2.3 to 3.4 mm; females from 3.0 to 4.0 mm. The length of the clypeal process of males is somewhat variable.

Diagnosis. The males of this species can readily be separated from *A. trigonum* by the difference in shape of the processes (Fig. 84). The radix of the palpus (Fig. 85) is much longer than wide and has several rows of evenly spaced denticles at its tip, whereas that of *A. baboquivari* is as wide as long. The epigynum (Fig. 88) has the median ridge shorter, higher and wider than in *A. trigonum*. The ridge is formed by the raised ends of the paired connecting canals; the opening is anterior but difficult to see. The ridge is about 0.06 mm wide while that of *A. baboquivari* is about 0.13 mm wide. The connecting canals (Fig. 87) are very short.

Natural History. (See introduction.)

Distribution. Southeastern United States, from South Carolina along the Gulf Shore of Mexico, south to El Salvador; southern California and the Greater Antilles; Map 3.

Records. United States. South Carolina. Charleston (J. H. Emerton). *Georgia.* Bibb Co.: near Macon. Burke Co.: between

Sardis and Waynesboro. Crisp Co.: Cordele. Lowndes Co.: near Valdosta (W. J. Gertsch). Screven Co.: N of Sylvania. Turner Co.: Ashburn (W. J. Gertsch). Ware Co.: Waycross (W. J. Gertsch). *Florida.* Alachua Co.: near Gainesville (R. V. Chamberlin). Collier Co.: Naples (R. Forster, W. J. Gertsch). De Soto Co.: near Arcadia (W. J. Gertsch). Highlands Co.: Lake Placid. Indian River Co.: Sebastian (G. Nelson). Jackson Co.: Marianna. Lake Co.: Leesburg (M. Statham). Lee Co.: Ft. Myers (W. M. Barrows). Levy Co.: Williston (R. V. Chamberlin). Saint Johns Co.: Hastings. *Alabama.* Baldwin Co.: Silver Hill (G. Nelson); Oak Air Park (A. F. Archer); Lagoon (A. F. Archer). Mobile Co.: near Chunchula (A. F. Archer). Morgan Co.: Decatur (A. F. Archer). *Mississippi.* Bolivar Co.: Shelby. Forrest Co.: Camp Shelby (A. F. Archer). Wilkinson Co.: Centreville. *Texas.* Anderson Co.: Palestine (O. Sanders). Atascosa Co.: near San Antonio (S. Mulaik). Bexar Co.: San Antonio. Cameron Co.: Arroyo Colorado (S. Mulaik); Harlingen (C. J. Goodnight). Frio Co.: Pearsall (L. I. Davis). Harris Co.: Houston (S. Mulaik). Harrison Co.: Marshall (S. Mulaik). Henderson Co.: 10 mi. E of Athens (O. Sanders). Hidalgo Co.: Weslaco (S. Mulaik); Edinburg (S. Mulaik); Mission (S. Mulaik). Jasper Co.: Jasper (S. Mulaik). Kleberg Co.: Kingsville (S. Mulaik). Newton Co.: Bon Wier. Polk Co.: Livingston (L. I. Davis). Starr Co.: Rio Grande City (S. Mulaik). Travis Co.: Onion Cr. (H. Frizzell); Austin (O. Sanders, H. E., D. L. Frizzell). *California.* Orange Co.: Laguna Beach, June 1931 (R. V. Chamberlin).

Mexico. Tamaulipas: Reynosa (S. Mulaik): near Villa Juárez (A. M., L. I. Davis). *Nuevo León:* Linares (L. I. Davis). *San Luis Potosí:* Valles (L. Steude); 36 km S of Valles (A. M. Davis). *Jalisco:* Ajijic (A. Archer). *Guerrero:* Omilteme (F. D. Godman. H. H. Smith). *Tabasco:* (O.P.-Cambridge, 1878). *Chiapas:* Las Cruces Arriaga (H. Wagner). *El Salvador:* Los Chorros, W of Santa Tecla, 700 m elev. (H. Peters).

Bahama Isl. Crooked Isl.: Major Cay Settlement (A. W. Scott). *Cuba.* Pinar del Río: San Vicente (A. F. Archer). Habana: Finca Somorrostro (A. F. Archer). Las Valles: Soledad (N. Banks). Oriente: Banes (A. F. Archer). *Jamaica:* St. Catherine Par.: Hellshire Hills; Pt. Henderson (A. F. Archer). *Haiti.* Port-au-Prince (A. F. Archer); Carrefour (A. F. Archer). *Dominican Republic.* Barahona Prov.: Sierra Martín García (A. F. Archer). Distrito de Santo Dominico: Boca Chica (A. M. Nadler); Ciudad Trujillo (A. M. Nadler). *Mona Isl.* (Serrallés).

Argyrodes baboquivari new species

Figures 89-94; Map 3

Type. Male from Molino Basin, Santa Catalina Mts., 1300 m elev., Pima County, Arizona, July 9, 1960 (J. A. Beatty), in the Museum of Comparative Zoology. The specific name is a noun in apposition, after the mountain range where the species is common.

Description. Male. Carapace yellowish with some light gray radiating lines. Sternum, legs yellow. Abdomen with pale grayish background and a large number of irregular silvery spots, sometimes with tan streaks. A dark patch between tips of bifurcation; dorsum with a median lanceolate mark. Cephalic process short and broad, its tip pointing forward and having some stiff setae (Fig. 89). Clypeal process long, similar to that of *A. furcatus,* but arising a little lower. Eyes small, subequal in size. Posterior median eyes about three diameters apart, one diameter from laterals. Abdomen as in other species, bifurcation sometimes barely visible. Total length of male holotype 3.5 mm. Carapace 1.4 mm long. First femur, 2.5 mm; patella and tibia, 2.6 mm; metatarsus, 1.2 mm; tarsus, 0.7 mm. The total length of this species varies from 3.3 to 4.5 mm.

Female. Color pattern as in male, but more variable and mostly pale. Abdomen very high so that tips are hardly posterior to spinnerets (Fig. 91). Some females almost lack the bifurcation. Total length of female 3.7 mm. Carapace 1.6 mm long. First femur, 3.2 mm; patella and tibia, 3.0 mm; metatarsus, 1.9 mm; tarsus, 0.9 mm. Length varies from 3.1 to 5.5 mm.

Diagnosis. This species is slightly larger than *A. furcatus;* the carapace of females is generally 1.4 to 1.6 mm long, that of *A. furcatus* less than 1.3 mm long in western Mexico. The eyes of females are larger, about two diameters apart; those of *A. furcatus* are more than two diameters apart. The cephalic process of the male is more pointed in front and a little longer and different in shape (Fig. 89). The radix of the male palpus is conspicuously wider with a median, toothed swelling (Fig. 90). The epigynum has the median raised area (Figs. 93, 94) larger, higher and more heavily sclerotized than in other species, and the openings are more ventral, larger and more easily seen. The width of the median raised area is about 0.12 mm, while in *A. furcatus* it is less than 0.06 mm. Females, however, may at times be difficult to separate from *A. furcatus.* Some specimens from Sonora have the median area bulging with the sides not well delineated.

Natural History. One female was collected from a "web between foliage and rock" by J. A. Beatty, a male from "under overhanging rock-ledge" in Arizona. The same collector found spiders "in *Latrodectus* web on rock," "in web on Agave along edge of dry wash," "in web in rocky ravine with *Diguetia, Theridion*" and "along with *Uloborus* in palm filled canyon" in Sonora.

Distribution. Southeastern Arizona, Chihuahua, Sonora; Map 3.

Records. United States. Arizona. Cochise Co.: South Fork, Cave Creek, near Portal, Sept. 11, 1950, June 10, 13, 1958 (W. J., J. W. Gertsch, Alexander). Graham Co.: Mt. Graham, July 14, 1956 (W. J. Gertsch, V. Roth). Pima Co.: Brown Canyon, Baboquivari Mts., June 9, 1960, ♀ ♂ (M. Cazier, W. J. Gertsch, R. Schrammel), July 19, 1959, ♀ ♂ (V. Roth); Bear Canyon, Santa Catalina Mts., 1700 m elev., Aug. 26, 1960, ♀ (J. A. Beatty); Molino Basin, Santa Catalina Mts., 1300 m elev., Aug. 3, 1960, ♀ ♂ paratypes (J. A. Beatty).

Mexico. Chihuahua: 5 km W of Matachie, July 7, 1947 (W. J. Gertsch). *Sonora:* mts. 26 km E of Magdalena, 1200 m elev., July 16, 1960, ♀ (J. A. Beatty); El Coyote, 28 km E of Río Bavispe, 1100 m elev., July 20-21, 1960, ♀ ♂ (J. A. Beatty).

Argyrodes concisus new species

Figures 56-60; Map 3

Type. Male from Tamazunchale, San Luis Potosí, Mexico, May 20, 1952 (M. Cazier, W. J. Gertsch, and R. Schrammel), in the American Museum of Natural History. The specific name is a Latin adjective meaning pruned or cropped, referring to the short head process.

Description. Carapace golden yellow with some gray on margins. Sternum yellow, reddish in center. Legs golden yellow with distal segments darker. Abdomen with pale gray background, overlaid with red posteriorly on dorsum, and sides covered with silvery markings. Thoracic groove not so conspicuous as in other species. Cephalic projection small, low and blunt. Clypeal projection also very small (Fig. 56). Eyes large with anterior medians much larger than others, separated by less than a diameter, almost touching laterals. Posterior median eyes separated by a little more than a diameter, about a radius from laterals. Abdomen with bifurcated tip as in other species. Total length 2.3 mm. Carapace 1.10 mm long. First femur, 1.96 mm;

patella and tibia, 2.00 mm; metatarsus, 1.18 mm; tarsus, 0.66 mm.

Female. Coloration similar to that of male. Eyes also large, anterior medians not quite a diameter apart, almost touching laterals. Posterior eyes as in male. Abdomen with two posterior dorsal tips (Fig. 58). Total length 3.5 mm. Carapace 1.55 mm long. First femur, 3.0 mm; patella and tibia, 2.6 mm; metatarsus, 1.4 mm; tarsus, 0.8 mm.

Diagnosis. Argyrodes concisus can be separated from *A. furcatus* and other species by the large eyes and short cephalic and clypeal projections (Fig. 56). Palpus (Fig. 57) similar to other species; the radix is short and narrow with denticles at its tip. The epigynum (Fig. 60) has a long median ridge, anterior to which are very indistinct openings.

Distribution. Northeastern Mexico; Map 3.

Records. Mexico. Veracruz: Tlapacoyan, 100 m elev., July 7-8, 1946, 2 ♀ (H. Wagner).

Argyrodes parvus (Exline), new combination

Figures 51-55; Map 3

Neospintharus parvus Exline, 1950, in Studies Honoring Trevor Kincaid, Univ. Washington Press, p. 112, pl. 1, figs. 2, 4. Female type from Prov. Guayas, Ecuador, lost.

Description. Male from Panama. Carapace, legs dusky yellow; cephalic projection orange. Sternum pale yellow. Abdomen with pale gray background, thickly covered with silvery spots, darker gray at tip and on lower sides. Cephalic projection wide, broadly rounded dorsally and projecting only slightly forward; clypeal projection short, pointing up (Fig. 51). Both projections with scattered setae. Eyes almost equal in size, lateral eyes almost touching. Posterior median eyes nearly three diameters apart. Abdomen extending high above and a little beyond spinnerets, wide and slightly bifurcate at tip. Total length 2.8 mm. Carapace 1.1 mm long. First femur, 2.2 mm; patella and tibia, 2.1 mm; metatarsus, 1.3 mm; tarsus, 0.7 mm. A male from Barro Colorado is darker with carapace mostly gray, legs brownish yellow and abdomen mostly dark gray with a pair of silvery white bands on each side of dorsum.

Female. Carapace brown and dark gray. Sternum reddish brown. Legs chestnut brown. Abdomen dark gray becoming reddish posteriorly and on venter, with a pair of large white bands on dorsum. Anterior median eyes a little larger than others; eyes spaced as in male, except that posterior medians are

not quite so far apart. Clypeus high and sloping. Abdomen as in male, wrinkled and slightly bifurcate at posterior tip (Fig. 53). Total length 3.9 mm. Carapace 1.4 mm long. First femur, 2.9 mm; patella and tibia, 2.6 mm; metatarsus, 1.5 mm; tarsus, 0.8 mm.

Diagnosis. The male is distinguished by the shape of the cephalic and clypeal projections (Fig. 51). The palpal radix is short with parallel sides, finely denticulate on its anterior margin. The embolus is long, narrow, with a pointed tip (Fig. 52). The inflated end of the conductor projects over the tip of the embolus. The female is difficult to distinguish from *A. trigonum* from the eastern United States and from *A. obscurus* from Peru. The genital area is pale with a very long, narrow median ridge (Fig. 55). The tubes are arched and longer than in related species, with the seminal receptacles a little over a radius apart (Fig. 54). It is not quite certain if the described specimens belong to *A. parvus* whose type is lost.

Distribution. Panama to Ecuador; Map 3.

Records. Panama. Boquete, Aug. 1939, ♂; Aug. 1950, ♀ (A. M. Chickering). *Panama Canal Zone.* Barro Colorado Isl., Aug. 1939, ♂ (A. M. Chickering).

Argyrodes trigonum (Hentz)

Figures 66-78; Map 3

Theridion trigonum Hentz, 1850, Jour. Boston Soc. Nat. Hist., vol. 6, p. 280, pl. 9, figs. 24, 25; 1875, The spiders of the United States, p. 152, pl. 16, figs. 24, 25; pl. 19, figs. 117, 131. Type from Alabama, lost.

Argyrodes trigonum, Emerton, 1882, Trans. Connecticut Acad. Sci., vol. 6, p. 23, pl. 5, fig. 1; 1902, The Common Spiders, p. 124, figs. 292-295. Simon, 1894, Histoire Naturelle des Araignées, vol. 1, p. 499, fig. 504. Roewer, 1942, Katalog der Araneae, vol. 1, p. 439, in part.

Argyrodes argyrodes, Keyserling, 1884, Die Spinnen Amerikas, Theridiidae, pt. 1, p. 181, pl. 8, fig. 109. Bonnet, 1955, Bibliographia Araneorum, vol. 2, pt. 1, p. 708, in part. Not *Argyrodes argyrodes* (Walckenaer).

Conopistha trigona, Kaston, 1948, Bull. Connecticut Geol. Nat. Hist. Surv., no. 70, p. 88, pl. 4, figs. 73-79.

Conopistha rufa, Archer, 1946, Paper Alabama Mus. Nat. Hist., no. 22, p. 26. Probably not *Linyphia rufa* Walckenaer, a *nomen dubium.*

Note. The specific name is used as a noun in apposition, as suggested by Bonnet, 1955.

Description. Male from Alabama. Carapace yellow with some gray except in head region. Sternum, legs yellow with some gray. Abdomen light gray with silvery spots and a large lanceolate

mark on dorsum; posterior darker than sides. Cephalic process unusually long and high, blunt and bearing setae at tip. Clypeus with a long, projecting median process, paralleling process of head. Clypeal process longer than in other species, slightly tapering toward tip where it is enlarged and bears setae (Figs. 66, 78). Eyes small. Anterior median eyes very close to laterals. Posterior median eyes separated by more than two diameters and nearly a diameter from laterals. Abdomen nearly triangular (Fig. 78). Total length 2.5 mm. Carapace 1.2 mm long. First femur, 2.6 mm; patella and tibia, 2.6 mm; metatarsus, 1.6 mm.

Female. Slightly darker and browner than male. Venter of abdomen darker than dorsum. Head region slightly elevated with narrow groove under eyes. Clypeus quite high, somewhat rounded underneath groove. Eyes similar to those of male. Abdomen with posterior bifurcation; extending well above and posterior to spinnerets (Figs. 69-73). Total length of a female from Alabama 4.2 mm. Carapace 1.5 mm long. First femur, 3.9 mm; patella and tibia, 3.6 mm; metatarsus, 2.2 mm; tarsus, 0.9 mm.

Variation. Size variation is slight in males, great in females. Coloration and shape of abdomen is extremely variable (Figs. 69-73). Some specimens have golden rather than silvery spots on the abdomen; in some specimens from Florida the posterior spots are overlaid with red. The abdomen is conspicuously bifurcate in many specimens, almost blunt in others. In some males the head process is longer than the clypeal process, in others the clypeal process is longer. Most males have a knob at the end of the clypeal process; some lack it. The male embolus varies somewhat in length; it may be as long as the radix. The epigynum varies depending on amount of sclerotization and whether or not the spider has mated.

Diagnosis. Males can be separated from related species by the shape of the cephalic and clypeal projections (Figs. 66, 78) and by the shape of the palpal parts (Fig. 67). The radix is wide, somewhat concave and has many denticles at its distal margin. The epigynum (Fig. 75) has a central selerotized area with a median ridge anterior to which are the openings. The seminal receptacles (Fig. 74) are their radius apart.

Natural History. Argyrodes trigonum is usually commensal in the webs of larger spiders, especially orb-weavers, but it has been collected also from webs of *Agelenopsis* and *Latrodectus.* Lamore (1958, Proc. Ent. Soc. Washington, vol. 60, p. 286) reports it as a frequent commensal in the webs of *Allepeira lemniscata* (Walckenaer) in Maryland, and in one case the host was eaten

by *A. trigonum*. Emerton collected it in the webs of *Theridion zelotypum* Emerton in Maine, in webs of *Linyphia marginata* C. L. Koch and *Agelenopsis* in Massachusetts. In Michigan it has been collected in pine forest, in hemlock, and probably in maple-basswood forest in Wisconsin. Beatty collected juveniles in hemlock-hardwood forest and in "short mine tunnel along with *Meta* and *Theridiosoma*" in Ohio.

Distribution. Ontario, eastern United States, from Maine to Florida, central Wisconsin, Arkansas to eastern Texas; Map 3.

Records. Canada. Ontario. Norfolk Co.: Turkey Pt. (A. Nadler). *United States. Maine.* Cumberland Co.: Casco Bay (J. H. Emerton). Piscataquis Co.: Katahdin Stream Camp, juv. (H., L. Levi). *New Hampshire.* Carroll Co.: Intervale (E. B. Bryant). Hillsborough Co.: Hollis. *Massachusetts.* Essex Co.: Amesbury (J. H. Emerton). *Connecticut.* New Haven (J. H. Emerton); South Meriden. *New York.* Cayuga Co.: Cayuga. Jefferson Co.: Woodville (S. C. Bishop). Nassau Co.: Sea Cliff, Hampstead Plains. Suffolk Co.: Cold Spring Harbor (J. H. Emerton). Tompkins Co.: Ithaca, West Danby. Yates Co.: Penn Yan. *New Jersey.* Ocean Co.: Lakehurst (J. Hallan). *Ohio.* Ashland Co.: Mohican Park, juv. (J. A. Beatty). Hocking Co.: Rockbridge. *Pennsylvania.* Columbia Co.: Orangeville. *West Virginia.* Pocahontas Co.: Minnehaha Springs (K. W. Haller). *Virginia.* Brunswick Co.: Alberta. Fairfax Co.: Falls Church (N. Banks). *Kentucky.* Breathitt Co.: Nobel (Buckhorn). Edmonson Co.: near Mammoth Cave. *Tennessee.* Grundy Co.: Beersheba. *North Carolina.* Avery Co.: Linville (J. H. Emerton). Buncombe Co.: Black Mountain (N. Banks); Ridgecrest (A. F. Archer). Durham Co.: Duke Forest (H., L. Levi). Guilford Co.: Greenboro (R. D. Barnes). Haywood Co.: Canton (N. Banks). Macon Co.: Highlands (A. F. Archer); Cullasaja Canyon (M. H., A. F. Archer). Yadkin Co.: Yadkinville. *Georgia.* Okefinokee Swamp. Rabun Co.: Clayton (J. C. Bradley). *Florida.* Alachua Co.: W of Gainesville. Highlands Co.: Sebring. Liberty Co.: Torreya State Park (W. J. Gertsch, R. Forster). Okaloosa Co.: Crestview (R. V. Chamberlin). *Alabama.* De Kalb Co.: De Soto State Park (A. F. Archer). Hale Co.: Moundville (A. F. Archer). Morgan Co.: Decatur (A. F. Archer); Trinity Mt. (M. Hanson, A. F. Archer). Tuscaloosa Co.: Tuscaloosa (A. F. Archer). ? Winston Co.: Bankhead Natl. For. (A. F. Archer). *Mississippi.* Wilkinson Co.: Centreville (A. F. Archer). *Michigan.* Crawford Co.: Hartwick Pines State Park, juv. (H., L. Levi). *Wisconsin.* Grant Co.: Wyalusing (H., L. Levi). Juneau

Co.: Rocky Arbor Park, juv. (H., L. Levi). Manitowoc Co.: Point Beach State Forest (H. Levi). Sauk Co.: The Dells (A. F. Archer); near North Freedom (A. Bakken). *Missouri.* Franklin Co.: Meramec Springs (H. E. Frizzell). Phelps Co.: Rolla (H. E. Frizzell). *Arkansas.* Washington Co.: 15 mi. S of Prairie Grove (M. Hite). *Texas.* Polk Co.: (R. H. Baker).

Argyrodes bicornis O.P.-Cambridge

Figures 95, 96; Map 3

Argyrodes bicornis O.P.-Cambridge, 1880, Proc. Zool. Soc. London, p. 334, pl. 29, fig. 12. Male type from Paraná [Brazil], in the Hope Department of Entomology, Oxford University, examined by Levi.

Note. F.P.-Cambridge (1902, Biologia Centrali-Americana, Araneidea, vol. 2, p. 404) synonomized *A. bicornis* with *A. trigonum* and other authors have followed. Examination of the type indicates that *A. bicornis* is distinct. This species is only known from the type specimen.

Diagnosis. Unlike most related species, *A. bicornis* has the head process slender. The clypeal process is of about the same width and length (Fig. 95).

Argyrodes rioensis new species

Figures 61-65; Map 3

Type. Male from Teresópolis, 1000 m elev., Est. Rio de Janeiro, Brazil, March 12, 1946 (H. Sick), in the American Museum of Natural History. The name is an adjective, referring to the state of Rio de Janeiro.

Description. Male. Carapace golden yellow, reddish on margin. Sternum, legs yellow with some darker marks, especially on sides and between spinnerets and posterior tip; venter with median brown stripe. Head process short, heavy, curved at its dorsum with its tip projecting anteriorly. Clypeal process (Fig. 61) some distance from head process, slender, directed slightly upward, bearing at its tip stiff setae that point at a right angle to axis of process. Anterior eyes a little larger than others, separated by about a diameter. Other eyes subequal. Posterior median eyes separated by about a diameter and a third, less than a radius from laterals. Bifurcation at tip of abdomen conspicuous. Total length of male 3.1 mm. Carapace 1.1 mm long. First femur, 1.90 mm; patella and tibia, 1.78 mm; metatarsus, 1.26 mm; tarsus, 0.70 mm.

Female. Color similar to that of male, except legs a little paler, abdomen with dorsal gray reticulation and usually with a black mark toward posterior tip. Venter densely infused with red, usually with a reddish median, longitudinal stripe. Clypeus with a deep groove below eyes, high and arched forward below. Eyes as in male. Abdomen heavy and high (Fig. 63). Total length 3.6 mm. Carapace 1.1 mm long. First femur, 2.4 mm; patella and tibia, 1.9 mm; metatarsus, 1.3 mm; tarsus, 0.8 mm. Length of females examined from 3.2 to 3.7 mm.

Diagnosis. Argyrodes rioensis is separated from *A. bicornis* by differences in the head processes of the males (Fig. 61). The male palpus (Fig. 62) has the radix blunter and longer, and tipped with denticles. The epigynum (Fig. 65) has a slightly raised median ridge with a single opening slightly anterior to the seminal receptacles.

Distribution. Southeastern Brazil; Map 3.

Records. Brazil. Ceara: Serra Communaty, ♀ (E. Gounelle, MNHN). *Rio de Janeiro:* Teresópolis, March 1946, ♀ ♂ paratypes (H. Sick). *Santa Catarina:* Nova Teutonia, lat 27°11′, long 52°23′, ♂ (F. Plaumann, SMF).

Argyrodes triangularis Taczanowski

Figures 97, 98; Map 3

Argyrodes triangularis Taczanowski, 1872 (1873), Horae Soc. Ent. Rossicae, vol. 9, p. 123, pl. 5, fig. 14. Male type from Cayenne, [French Guiana], in the Polish Academy of Sciences, Warsaw, examined by Levi. Keyserling, 1884, Die Spinnen Amerikas, Theridiidae, pt. 1, p. 200, pl. 9, fig. 120.

Description. Male from Panama. Carapace and legs orange-yellow with a little gray. Sternum reddish orange. Abdomen pale gray with red on lower sides extending to dorsum posteriorly; posterior side and venter pale with large silvery patches. Head process narrowed to a point with stiff setae overlapping those on tip of clypeal process. Head process of type thicker at base (Fig. 97). Clypeal process very slender, longer than cephalic process except in type specimen. Eyes small except anterior medians; those of each side close together; posterior medians separated by two diameters. The abdomen (except in the type specimen) is bluntly bifurcate at posterior tip. Total length 3.2 mm. Carapace 1.3 mm long. First femur, 2.6 mm; patella and tibia, 2.5 mm; metatarsus, 1.4 mm; tarsus, 0.7 mm.

Figures 97, 98 were prepared from the type of *A. triangularis*.

Diagnosis. Although the Panamanian specimen differs in minor ways from the type, its identification as *A. triangularis* seems quite certain. The head and clypeal processes are diagnostic (Fig. 97). The palpal radix is expanded at the tip so that its mesal margin is almost at right angles to long axis of palpus, and the distal margin is finely denticulate. The widely expanded tip of the conductor touches the distal end of the long, narrow embolus (Fig. 98).

Distribution. Panama, French Guiana; Map 3.

Record. Panama Canal Zone. Barro Colorado Isl., July 1939, ♂ (A. M. Chickering).

The *Ariamnes* Group

Argyrodes longissimus (Keyserling), new combination

Figures 100-109; Map 4

Ariamnes longissimus Keyserling, 1891, Die Spinnen Amerikas, Brasilianische Spinnen, p. 202, pl. 7, fig. 145. Male and female syntypes from N. Freiburg [Nova Friburgo, Est. Rio de Janeiro], Espírito Santo, and St. Antonio on the Rio Pomba [Est. Rio de Janeiro], Brazil, in the British Museum (Natural History). Specimens examined by Levi. Göldi, 1892, Mitt. Osterlande, neue Folge, vol. 5, p. 224, 230, 233.

Description. Male from Est. Santa Catarina, Brazil. Carapace dusky yellow with a paler median band. Clypeus, chelicerae, proximal segments of palpi and sternum pale yellow. Legs dusky yellow with proximal segments of anterior legs yellowish brown. Abdomen grayish white with posterior part speckled gray. Carapace low and flat, slightly raised in eye region, with central tuft of curved setae between anterior lateral eyes (Fig. 101). Eyes all small, anterior and posterior median eyes about equal in size. Median ocular area square, eyes separated by more than a diameter and a half. Clypeus slightly concave below eyes, projecting above chelicerae. Chelicerae small and short. Legs moderately robust; anterior legs with enlarged setae under distal end of tibiae. One or two somewhat enlarged setae under proximal end of anterior metatarsi. Abdomen cylindrical, very long, tapering to sharp point, covered with setae, with cuticle showing some annulations. Total length, approximately 18.5 mm. Carapace 1.9 mm long. First femur, 5.7 mm; patella and tibia, 5.0 mm; metatarsus, 2.9 mm; tarsus, 1.5 mm. Another male is much paler than the one described.

Female from São Paulo, Brazil. Female colored like male but a little darker with an orange cast. Abdomen orange, thickly covered with golden flecks. Carapace as in male but with cephalic region low. Clypeus low, with very shallow groove under eyes. Chelicerae more robust than in male. Eyes small as in male but a little closer together. Abdomen even more elongate than in male (Fig. 100), with a pair of small dorsal sclerotized patches at base. Total length, approximately, 24.0 mm. Carapace 2.2 mm long. First femur, 7.5 mm; patella and tibia, 6.4 mm; metatarsus, 3.8 mm; tarsus, 1.6 mm.

Figures 102 and 108 were prepared from the syntypes.

Variation. The palpi of four males from different localities were not alike (Figs. 102-105). Two males from Est. Santa Catarina had similar palpi. The internal genitalia of two females differed (Figs. 106, 107). Too few specimens were available to decide whether there are several species or a single polymorphic species and most males and females were not collected together. We are treating the specimens as a single variable species.

Diagnosis. Argyrodes longissimus differs from *A. attenuatus* principally in structures of the genitalia. The radix of the male palpus is short and stout, with distal end broad. The embolus is drawn out into a long, heavy, curved tube (Figs. 102-105); partly hidden dorsally is the large thumb-like process of the embolus. The conductor is short, fleshy, and touches the embolus. The epigynum of the female has a protruding horizontal bar and the cuticle anterior to it is transversely ribbed (Figs. 108, 109). Openings to the tubes are posterior to bar. Tubes are wider than in *A. attenuatus,* tapering, and reach anterior end of receptacles (Figs. 106, 107). In some females the receptacles are curved toward one another.

Natural History. Göldi (1892), who collected specimens for Keyserling, reports that when touched, the spider moves its whip-like tail like an earthworm. "I have questioned why this adventurous long tail could be of special use, without obtaining an answer. Everytime I obtained an *Ariamnes* by beating in the virgin forest, I was reminded of some of the smaller and delicate walking sticks of the genus *Bacillus*" (freely transl.).

Distribution. Southern Brazil; Map 4.

Records. Brazil. Espírito Santo: Santa Teresa, Jan. 26, 1959, ♂ (A. M. Nadler). *Minas Gerais:* Miracema on Rio Pomba (Göldi, 1892). *Rio de Janeiro:* near Santo Eduardo (Göldi, 1892); Colonia Alpina [Teresópolis], ♀ ♂ (E. Göldi, MNHN); Teresópolis, Nov. 1945, ♀ ♂, March 1946, ♀ (H. Sick). *São Paulo:* Jabaquara, Cidade São Paulo, Dec. 1945, ♀, juv. (H.

Sick). *Santa Catarina:* Nova Teutonia, lat 27°11′, long 52°23′, 2 ♂, juv. (F. Plaumann, SMF).

Argyrodes haitensis new species

Figures 110, 111; Map 4

Type. Female from 32 km from Aux Cayes, 330 m elev., Haiti, Aug. 28-29, 1935 (W. G. Hassler), in the American Museum of Natural History. The species is named after the type locality.

Description. Female. Carapace, sternum, mouthparts and legs bright yellow with a pair of narrow curved gray stripes posterior to eyes, and gray infusions opposite coxae on carapace. Abdomen very pale yellow anteriorly, becoming darker posteriorly, almost completely covered with silvery spots arranged in longitudinal rows. Carapace flat. Clypeus slightly higher than diameter of anterior median eyes, a little rounded with a very shallow groove under eyes, and leaving a gap between lower edge and base of chelicerae. Chelicerae short, robust. Eyes approximately equal in size; anterior medians separated by more than a diameter. Median eyes forming a square, very near lateral eyes. Region between anterior median eyes slightly protruding. Abdomen narrow, cylindrical, pointed at posterior tip and having some setae but without cuticular wrinkles. Total length approximately 30 mm. Carapace 1.9 mm long. First femur, 6.4 mm; patella and tibia, 5.5 mm; metatarsus, 3.4 mm; tarsus, 1.4 mm.

Variation. Female paratype with anterior median eyes larger than others, and area between them slightly raised.

Diagnosis. Argyrodes haitensis is similar to *A. approximatus.* The tubes of the epigynum are very slender with widely separated openings. Seminal receptacles elongate as in *A. approximatus,* but bent, meeting tubes halfway to openings, separated and somewhat bulging in middle (Fig. 110). The male is unknown.

Records. Haiti. 40 km from Aux Cayes, 660-1000 m elev., Aug. 29, 1935, ♀ paratype (W. G. Hassler).

Argyrodes mexicanus new species

Figures 99, 112-115; Map 4

Type. Female from Villa Santiago, Horsetail Falls, 650 m elev., Nuevo Léon, Mexico, June 19, 1940 (H. Hoogstraal), in the Museum of Comparative Zoology. The name is a latinized adjective.

Description. Male from San Luis Potosí. Carapace dusky yellow with a paler median stripe, paler in cephalic region, clypeus and chelicerae. Sternum, legs brownish orange. Abdomen yellowish orange. Carapace flat and low, slightly elevated in eye region with setae on highest point (Fig. 112). Clypeus straight, moderately high with some setae. Anterior median eyes largest. Lateral eyes touching and smaller than posterior median eyes. Legs more robust than in related species. Abdomen very long, cylindrical, gently tapering. Total length approximately 25 mm. Carapace 1.3 mm long. First femur, 4.7 mm; patella and tibia, 3.8 mm; metatarsus, 2.6 mm; tarsus, 1.3 mm.

Female type colored like male. Abdomen thickly covered with golden flecks dorsally, silvery flecks ventrally. General structure as in male, except in eye region which is not elevated. Abdomen cylindrical, gently tapering, with rounded rather than pointed tip as in most species (Fig. 99). Total length approximately 40 mm. Carapace 2.6 mm long. First femur, 8.3 mm; patella and tibia, 6.6 mm; metatarsus, 4.7 mm; tarsus, 1.8 mm.

Diagnosis. The epigynum (Fig. 115) is flat with a curved transverse sclerotized ridge, some distance anterior to genital groove. The openings are anterior to ridge. Seminal receptacles are visible through the cuticle. Unlike other American species seminal receptacles are pear-shaped with tubes narrow throughout (Fig. 114). Unlike that of *A. attenuatus,* the embolus of the male palpus is diamond-shaped (Fig. 113). The radix is extended at its distal tip and slightly tuberculate.

Natural History. The male was collected in grass and wood under waterfall.

Distribution. Northern Mexico; Map 4.

Records. Mexico. San Luis Potosí: El Salto, Nov. 13, 1959, ♂ (C., S. Bolívar, J. M. Molina).

Argyrodes attenuatus (O.P.-Cambridge), new combination

Figures 118-127; Map 4

Ariamnes attenuatus O.P.-Cambridge, 1881, Proc. Zool. Soc. London, p. 770, pl. 66, fig. 3. Male, female syntypes from Amazons, Brazil, in the Hope Department of Entomology, Oxford University, examined by Levi. Bonnet, 1955, Bibliographia Araneorum, vol. 2, pt. 1, p. 739. Di Caporiacco, 1948, Proc. Zool. Soc. London, vol. 118, p. 650. Kritscher, 1957, Ann. Naturhist. Mus. Wien, vol. 61, p. 271, figs. 31, 32.

Ariamnes gracillima O.P.-Cambridge, 1894, Biologia Centrali-Americana, Araneidea, vol. 1, p. 129, pl. 17, fig. 9. Female type from Los Remedios

in Chiriquí, Panama, in the British Museum (Natural History), examined by Levi. F.P.-Cambridge, 1902, Biologia Centrali-Americana, Araneidea, vol. 2, p. 408, pl. 38, fig. 20. NEW SYNONYMY.

Ariamnes approximata O.P.-Cambridge, 1894, *op. cit.*, p. 130, pl. 17, fig. 8. Juvenile female (before final molt) type from Bugaba, Chiriquí, Panama, in the British Museum (Natural History), examined by Levi. F.P.-Cambridge, 1902, *op. cit.*, p. 408. NEW SYNONYMY.

Ariamnes longissimus, Simon, 1897, Proc. Zool. Soc. London, p. 521. Not *A. longissimus* Keyserling.

Ariamnes pulcher Soares and Camargo, 1948, Bol. Mus. Paraense, vol. 10, p. 364, fig. 13. Male type from Chavantina, Mato Grosso, Brazil, in the Departamento de Zoologia, Secretaria da Agricultura, São Paulo. NEW SYNONYMY.

Ariamnes sinuates Schenkel, 1953, Verh. Naturf. Gesell. Basel, vol. 64, p. 10, fig. 10. Male type from near El Pozón, Dto. Acosta, Prov. Falcon, Venezuela, in the Naturhistorisches Museum, Basel, examined by Levi. NEW SYNONYMY.

Description. Male from Panama Canal Zone. Carapace yellow with marginal gray lines. Sternum pale yellow with median longitudinal gray line. Legs yellow, palpi nearly white except yellow and brown tarsi. Abdomen very pale yellow anteriorly infused with some gray, becoming completely gray beyond spinnerets and dotted with dark gray spots and silvery flecks. Carapace very low and flat, raised in median ocular area and between anterior median eyes. Highest point tipped with a small tuft of stiff anteriorly curved bristles; on its anterior face at level of the median anterior eyes a group of dorsally curved setae arises from a low keel (Fig. 118). Anterior and posterior median eyes equal in size. Eyes of each side close together; posterior medians separated by a diameter and a half. Clypeus high, straight, somewhat swollen above. Legs very slender, covered with short setae. Distal end of tibiae I and II with a group of spines underneath. Metatarsi I and II with a short heavy spine underneath at proximal end. Abdomen cylindrical. Cuticle of tail with annulate wrinkles, and thickly covered with long, fine setae. Tip of abdomen pointed. Abdomen often curled in alcoholic specimens. Total length 9.3 mm. Carapace 1.5 mm long. First femur, 5.9 mm; patella and tibia, 5.5 mm; metatarsus, 2.8 mm; tarsus, 1.5 mm.

Female from same locality. Color as in male with genital area orange. Carapace as in male but only slightly elevated and rounded between eyes. Eyes as in male. Clypeus lower, straight. Cheliceral fang groove with one tooth on each margin. Legs I and II without spines. Abdomen as in male, but longer and often

thicker (Fig. 127). Total length 16.5 mm. Carapace 2.1 mm long. First femur, 7.7 mm; patella and tibia, 7.1 mm; metatarsus, 4.0 mm; tarsus, 1.8 mm.

Variation. Southern specimens are slightly larger. The palpi of males seem alike (except for a male syntype specimen whose ducts seem slightly longer), the loop in the tegulum almost touching the large mesal portion of the duct, and the portion of the duct proximal to the loop being slightly wavy. There is, however, considerable variation in the epigyna. The projecting knob of the epigynum varies in shape; some individuals have the raised armlike anterior extensions long, others very short (Figs. 124, 125). There is considerable variation in shape of the seminal receptacles (Figs. 121-123).

Diagnosis. The palpus of *A. attenuatus* males bears a long armlike radix, widened, somewhat twisted and bordered at its tip with a comb of short, recurved setae. The embolus is flat with its mesal side extended into a long rounded arm, dorsally and anteriorly directed. A long stiff anterior spine bears the duct. The fleshy conductor is short, thumb-like, somewhat variable. The median apophysis is conspicuous, swollen at its anterior end (Figs. 119, 120). The epigynum has a projection with a round opening near the margin, and lateral ridges (Figs. 124, 125). Internally a pair of greatly elongated parallel seminal receptacles are close together. The tubes enter anteriorly and on the ectal side. Unlike *A. longissimus* the diameter of the tubes is about the same throughout (Figs. 121-123). The swelling in the eye region of *A. attenuatus* (Fig. 118) is different from that of *A. schlingeri.*

Natural History. Two egg cases filled with spiderlings were collected with a male and female *A. attenuatus* at Barro Colorado Island, July 1936 by A. M. Chickering. These are pale yellow, elongate, purse-like, approximately 48 mm long, 1½-2 mm wide (Fig. 3).

Distribution. Costa Rica, Lesser Antilles to Argentina; Map 4.

Records. Costa Rica. (SMF); Turrialba (Tristan), May 1944 (F. Schrader); San Isidro del General, 700-1400 m elev. (D. Rounds). *Panama Canal Zone.* Madden Dam, Sept. 6, 1956 (W. Lundy); Barro Colorado Isl. (many collections, A. M. Chickering); Forest Reserve (A. M. Chickering); Madden Dam (A. M. Chickering). *Lesser Antilles. St. Vincent Isl.* (H. H. Smith, BMNH). *Grenada.* Grand Etang, Sept. 1910 (R. Thaxter). *Colombia. Caqueta:* Río Orteguaza, 200 m elev., Aug.-Sept. 1947 (L. Richter). *Venezuela.* "La Guiaira, Tovar, San Esteban,"

1888 (E. Simon, MNHN). *Monagas:* Caripito, March 1942 (W. Beebe). *Aragua:* Maracay (SMF). *British Guiana.* Rockstone, Essequebo Riv., June 26, 1927 (P. Babiy); Rupununi Riv., near Mt. Makarapan, Oct. 5, 1937 (W. G. Hassler). *Surinam.* Para Dist., Apr. 21, 1927. *Peru. Loreto:* Iquitos, May 1920 (H. S. Parrish); Salt mine far up Río Pisqui, Sept. 1929 (H. B.). *Junín:* Huacapistana, Río Tarma, June 1-2, 1920; Colonia del Perené, June 18-20, 1920. *Brazil. Amapá:* Oiapoque, May 1959 (M. Alvarenga). *Ceara:* Serra Communaty (E. Gounelle, MNHN). *Guapuré:* Villa Murtinho, March-April 1922 (J. W. Williamson); Abunã, March 1922 (J. H. Williamson). *Amazonas:* ? Taperinha (Kritscher, 1957). *Paraguay.* Río Apa. *Alto Paraná:* Taguararapa. *Bolivia. Beni:* Rurrenabaque, Nov. 10, 1956 (L. Peña, ISNB). *Argentina. Jujuy:* San Juancito, Feb. 1920 (Cornell Univ. Exped.).

Argyrodes schlingeri new species

Figures 116, 117; Map 4

Type. Male from Yurac, 110 km east of Tingo María, Dept. Huánuco, Peru, Sept. 28, 1954 (R. I. Schlinger, E. S. Ross), in the California Academy of Sciences. This species is named for Mr. R. I. Schlinger.

Description. Carapace dusky yellow, paler in midline and in cephalic region, on clypeus, chelicerae, and proximal segments of palpi. Sternum yellow. Abdomen gray, thickly covered with dull silvery spots. Carapace flat with slight transverse ridge bearing setae in cephalic region. Clypeus short, rounded, projecting above chelicerae, bearing curved setae (Fig. 116). Anterior and posterior median eyes subequal in size. Eyes more widely separated than in related species. Anterior median eyes separated by more than a diameter. Chelicerae small. Legs slender, with anterior tibiae bearing spines at distal end on venter, but none on metatarsi. Abdomen very long and slender, cylindrical and tapering to sharp point, thickly covered with fine setae. Total length, approximately, 20 mm. Carapace 1.7 mm long. First femur, 6.3 mm; patella and tibia, 5.3 mm; metatarsus, 3.0 mm; tarsus, 1.6 mm.

Diagnosis. Argyrodes schlingeri males are distinct from males of *A. attenuatus* in lacking the distal angle in the palpal radix, and in having the tubes in the tegulum and median apophysis longer and more tortuous (Fig. 117).

The *A. argyrodes* species group

Argyrodes argyrodes (Walckenaer)

Figures 151-153

Linyphia argyrodes Walckenaer, 1841, Histoire Naturelle des Insectes Aptères, vol. 2, p. 282. Type locality here designated as Algeria, specimens lost. Vinson, 1863, Aranéides des îles de la Réunion, Maurice et Madagascar, Paris, p. 274.

Linyphia gibbosa Lucas, 1846, Histoire Naturelle des Animaux articulés *in* Exploration scientifique de l'Algérie, Zool., vol. 1, p. 254. Types from Algeria.

Argyrodes gibbosus, Simon, 1873, Mém. Soc. royal sci. Liége, ser. 2, vol. 5, p. 129. Bonnet, 1955, Bibliographia Araneorum, vol. 2, p. 712.

Argyrodes argyrodes, Simon, 1881, Les Arachnides de France, vol. 5, p. 16. F.P.-Cambridge, 1902, Biologia Centrali-Americana, Araneidea, vol. 2, pl. 38, figs. 9, 10. Roewer, 1942, Katalog der Araneae, vol. 1, p. 430.

Note on nomenclature. Although this is the type species of the genus, there has been considerable confusion about the application of the name. Walckenaer, in the original description, mentions Abbot's drawings of Georgia spiders in America, as well as specimens from France. However, Walckenaer states: "L'individu que j'ai décrit se trouvait dans ma collection, dans une bouteille, avec plusieurs Aranéides de France; cependant il serait possible qu'il provint de l'Algérie ou de la Guadeloupe [West Indies]. Dans cette incertitude, la figure d' Abbot ne différant que faiblement de celle-là, je n'ai pas dû les distinguer spécifiquement." Vinson, 1863, as first reviser, interpreted *L. argyrodes* as a European or African species, although the type locality was uncertain. This interpretation makes *A. gibbosus* (Lucas) a synonym of *A. argyrodes* (Walckenaer), and makes *A. elevatus* Taczanowski the name of the species found in America and first observed by Abbot in Georgia.

Distribution. Southern France (Provence); southern Europe, North Africa, probably all Mediterranean countries.

Argyrodes elevatus Taczanowski

Figures 128-132; Map 5

Linyphia argyrodes Walckenaer, 1841, Histoire Naturelle des Insectes Aptères, vol. 2, p. 282. In part, Abbot's drawings of specimens from Burke County, Georgia.

Argyrodes elevatus Taczanowski, 1872 (1873), Horae Soc. Ent. Rossicae, vol. 9, p. 120, pl. 5, fig. 12. Female holotype from Uassa, French Guiana [Rio Uaça, Amapa, Brazil], in the Polish Academy of Sciences,

Warsaw, examined by Exline and Levi. Keyserling, 1884, Die Spinnen Amerikas, Theridiidae, pt. 1, p. 188, pl. 9, fig. 112. Bonnet, 1955, Bibliographia Araneorum, vol. 2, pt. 1, p. 711.

Argyrodes nephilae, Keyserling, 1884, *op. cit.*, p. 184, pl. 8, fig. 110. Not *A. nephilae* Taczanowski. (Specimens of Keyserling in very poor condition, thus determination uncertain.)

Argyrodes concinnus O.P.-Cambridge, 1880, Proc. Zool. Soc. London, p. 322, pl. 28, fig. 2. Male holotype from the Amazons in the Hope Department of Entomology, Oxford University, examined by Levi.

Argyrodes jucunda O.P.-Cambridge, 1880, *op. cit.*, p. 326, pl. 28, fig. 6. Female holotype from Paraná [Brazil], in the Hope Department of Entomology, Oxford University, examined by Levi. Bonnet, 1955, *op. cit.*, p. 714.

Argyrodes lugens O.P.-Cambridge, 1880, *op. cit.*, p. 327, pl. 28, fig. 2. Female holotype from the Amazons, in the Hope Department of Entomology, Oxford University.

Argyrodes piraticum McCook, 1890, American Spiders, vol. 2, p. 388, *nomen nudum*. California. NEW SYNONYMY.

Argyrodes decorus Banks, 1908, Canadian Ent., vol. 40, p. 207. Female holotype from San Pedro, [Los Angeles], California, in the Museum of Comparative Zoology, examined by Levi. NEW SYNONYMY.

Argyrodes pulcherrima Mello-Leitão, 1917, Broteria, vol. 15, p. 86, figs. 7, 8. Female type from Manguinhas, Distrito Federal, [Brazil]. NEW SYNONYMY.

Argyrodes bielavis Chamberlin, 1924, Proc. U.S. Natl. Mus., vol. 63, art. 13, no. 2481, p. 5, pl. 1, figs. 2-5. Male holotype from Aimesville [? Aimwell], Louisiana, in the Museum of Comparative Zoology, examined by Levi. NEW SYNONYMY.

Argyrodes cingulatus Petrunkevitch, 1925, Trans. Connecticut Acad. Sci., vol. 27, p. 98, figs. 3-5. Female holotype from Panama City, Panama, in the Petrunkevitch personal collection, examined by Exline.

Argyrodes falcatus Badcock, 1932, Jour. Linn. Soc. London, zool., vol. 38, p. 9, figs. 4a-e. Female holotype from Makthlawaiya, Paraguay, lost. NEW SYNONYMY.

Argyrodes rotundus Caporiacco, 1938, Atti Soc. Italiana Sci. Nat., vol. 77, p. 264. Female holotype from Presidio Isl., Lago de Chapala, Jalisco, Mexico, in the collection of the Zoological Institute, Bologna, examined by Levi. NEW SYNONYMY.

Conopistha elongata Bryant, 1940, Bull. Mus. Comp. Zool., vol. 86, p. 306, pl. 5, figs. 68, 69, 75, 76. Male holotype from Soledad [Las Villas], Cuba, in the Museum of Comparative Zoology, examined by Levi.

Conopistha argentinus Mello-Leitão, 1941, Rev. Mus. La Plata, n.s., vol. 2, p. 143, fig. 39. Male holotype from Mojón, Salta, Argentina, in the Museo de La Plata, examined by Levi. NEW SYNONYMY.

Conopistha nephilae, Bryant, 1942, Bull. Mus. Comp. Zool., vol. 89, p. 339, figs. 15, 16. Chamberlin and Ivie, 1944, Bull. Univ. Utah, biol. ser., vol. 8, no. 5, p. 37. Archer, 1946, Paper Alabama Mus. Nat. Hist., no. 22, p. 27, pl. 2, fig. 5. Not *A. nephilae* Taczanowski.

Conopistha argyrodes nephilae, Exline, 1945, Ann. Ent. Soc. America, vol. 38, p. 510, pl. 1, figs. 1-14; pl. 2, figs. 15-17. Kraus, 1955, Abhandl. Senckenbergischen Naturf. Gesell., no. 493, p. 15, figs. 27-29. Not *A. nephilae* Taczanowski.

Rhomphaea simplex Caporiacco, 1954, Comm. Acad. Pontificia Sci., vol. 16, p. 72, fig. 10. Female holotype from Uanary, French Guiana, in the Muséum National d'Histoire Naturelle, Paris, examined by Levi. NEW SYNONYMY.

Conopistha jucunda, Kritscher, 1957, Ann. Naturhist. Mus. Wien, vol. 61, p. 271, fig. 30.

Description. Male from Panama. Carapace, sternum, legs yellow, gray shading on posterior part of carapace and sternum. Abdomen nearly white on sides with silvery flecks, dark gray on venter and on middorsal line and posterior tip. Other males from pale white carapace and legs, to brown or dark gray. Carapace projecting anteriorly, bulbous at end bearing anterior median eyes. Clypeal projection parallel under the cephalic projection, leaving some space between them proximally but touching in middle, bending dorsally at end, slightly longer than cephalic projection (Fig. 128). Total length 4.0 mm. Carapace 2.2 mm long. First femur, 3.3 mm; patella and tibia, 3.6 mm; metatarsus, 2.9 mm; tarsus, 1.3 mm.

Female from Panama. Coloration similar to that of male but more variable. More mature specimens having abdomen with black flecks and oblique stripes of silver, or silver with broad oblique bands of black, or nearly all black. Legs annulate or black. Total length 3.4 mm. Carapace 1.5 mm long. First femur, 2.6 mm; patella and tibia, 2.8 mm; metatarsus, 2.3 mm; tarsus, 1.0 mm.

Variation. Young females are often difficult to separate from *A. nephilae;* they are, however, always larger. Older females have massive abdomens. With increasing maturity there is an increase in pigmentation (Exline, 1945).

While there is little variation in palpal structures of males, there is some variation in the thickness and length of the cephalic projection of the carapace. In some specimens the cephalic projection is slightly elevated, occasionally arched, rarely depressed. The position of the posterior median eyes is variable, sometimes at the base of the projection, sometimes on it.

A male from Baldwin County, Alabama, measured 3.3 mm long, with cephalic projection slightly elevated, arched and nearly as long as the clypeal process. Female, 3.5 mm long, with venter of abdomen pale, has sides partially black with reddish streaks and the rest silvery. Another female, 3.8 mm long,

with abdomen very high and pointed, is entirely silvery. Females from Travis County, Texas, measured from 4.0 to 5.2 mm long, all with silvery abdomens, pointed high above and behind spinnerets; two specimens have sides obliquely streaked with brown. Males from Bahama Islands, 2.7 to 4.3 mm long; females, 2.5 to 4.8 mm long. A majority of the Bahama Island specimens has the sides of abdomens obliquely striped with black; one all black with silvery tip and scattered flecks of silver. Males from Victoria, Tamaulipas 3.6 mm long; females, 3.3 to 4.3 mm long. Males from Galapagos Islands 3.4 to 3.6 mm long; the cephalic projection in one specimen is very slightly depressed, short and thick; a female, 2.6 mm long with high, heavy, black abdomen, has silvery spots. A male from Rio de Janeiro, Brazil, is 3.6 mm long; another, 3.5 mm long, with cephalic projection and clypeal process both shorter than usual. Males from Apa, Paraguay, 3.3 to 4.0 mm long. Two males of this collection have short, thick cephalic projection with almost no opening between it and the clypeal projection; females, 2.5 to 3.7 mm long. Panamanian males measure from 3.4 to 4.0 mm; females, 2.5 to 4.7 mm long.

Diagnosis. The radix of the palpus is long (Fig. 129) with a rugose triangular tip, a large dorsal tooth at right angles to the long axis, and a line or carina running from tip to base. Embolus large, with process bearing distal part of duct well separated from median tooth. Epigynum (Fig. 132) dark, raised, heavily sclerotized, somewhat rugose with fossae widely separated. The area occupied by the seminal receptacles is much narrower than that occupied by fossae. It is assumed that some differences in the genital plate are due to varying ages of individuals, the more sclerotized plates occurring in older specimens.

Natural History. This species is often found in the web of *Nephila* (Alabama, Panama, Haiti, Cuba) and has also been found in the webs of *Argiope argentata* (Fabricius) in California.

Distribution. Southern United States (rare in West), south to Peru and Argentina, Galapagos Islands; Map 5.

Records. United States. Virginia. Fairfax Co.: Falls Church (N. Banks). *North Carolina.* Carteret Co.: Carrot Isl. (R. D. Barnes). Wake Co.: Raleigh (C. S. Brimley). *South Carolina.* Charleston (J. H. Emerton). *Georgia.* Jefferson Co.: Wrens (W. Ivie). *Florida.* Alachua Co.: Gainesville (H. K. Wallace). Marion Co.: (H. K. Wallace). Orange Co.: 7 mi. E of Apopka (Nirenberg). Putnam Co.: Palatka (R. V. Chamberlin). St. Johns Co.: St. Augustine (R. V. Chamberlin). *Alabama.* Baldwin Co.: Lagoon (A. F. Archer); Silverhill (G. Nelson). Houston Co.: Big Creek (A. F. Archer). Mobile Co.: N of Bucks

(A. F. Archer); NE of Theodore (A. F. Archer). Montgomery Co.: Mt. Meigs (A. F. Archer). Tuscaloosa Co.: Tuscaloosa (A. F. Archer). *Mississippi.* Lee Co.: Auburn (N. Banks). Wilkinson Co.: Centreville (A. F. Archer). *Missouri.* Phelps Co.: Rolla (V. Roth, H. E., D. L. Frizzell). *Louisiana.* 4 mi. SE of Natchitoches (T. H. Hubbell). *Texas.* Cameron Co: Harlingen (D. E. Hardy). Comal Co.: New Braunfels (E. S. Ross). Denton Co.: Lake Dallas (S. E. Jones). Hidalgo Co.: S of Pharr (S. Mulaik); Edinburg (S. Mulaik); Arroyo Colorado (S. Mulaik). Starr Co.: 5 mi. E of Rio Grande City (S. Mulaik). Travis Co.: Onion Creek (H. E. Frizzell); Austin (D. L., H. E. Frizzell). *California.* Los Angeles. Orange Co.: Dana Pt. (W. Ivie). San Diego Co.: mouth of San Diego River. Ventura Co.: SE of Carpinteria (W. J. Gertsch, V. Roth).

Mexico. Tamaulipas. Reynosa (W. Green); Soto La Marina; La Victoria (both M. Cazier et al.). *Sinaloa.* 64 km S of Culiacán (W. J. Gertsch). *San Luis Potosí.* Huichihuayán (M. Cazier et al.). *Morelos.* Cocoyoc (W. J. Gertsch, V. Roth). *Veracruz.* (?) Plan del Río (V. Roth, W. J. Gertsch); Fortín (L. I. Davis). *Chiapas.* Tonalá (A. Petrunkevitch). *Campeche.* Lerma (C., M. Goodnight); Campeche (H. Wagner). *El Salvador.* (Kraus, 1955). *Panama Canal Zone.* Barro Colorado Isl. (many coll.); Fort Randolph; Forest Reserve; Porto Bello; Pedro Miguel; Summit, near Cocoli; Arraijan; France Field; Port Sherman (all A. M. Chickering); Gamboa (W. Lundy); Ancón (N. Banks). *Panama.* Old Panama (C. D. Michener); Panama City (C. D. Michener); El Valle (A. M. Chickering); Tobago Isl., Panama Bay. *Bahama Islands.* Long Isl.; Rum Cay (L. Giovannoli); Green Turtle Cay (A. Rabb); Santo Domingo (K. P. Schmidt); Cat Isl. (E. B. Hayden); West Caicos Isl. (Hayden et al.); Great Inagua Isl. (E. B. Hayden); Crooked Isl. (A. W. Scott, Jr.). *Cuba.* San Pedrito, Oriente (A. F. Archer); "Columpo," Isla de Pinos (A. F. Archer). *Jamaica.* Kingston Par.: Palisadors Area (A. M. Chickering). St. Catherine Par.: Hellshire Hills (A. F. Archer). *Haiti.* Gonave Isl. (J. G. Myers); Dame-Marie (A. Audant). Port au Prince (A. F. Archer). Petionville (A. F. Archer). *Dominican Republic.* La Romana (Hassler); Porto Plata (D. Hurst, MNHN); Trujillo Valdez (A. F. Archer). *Mona Isl.* (sev. coll.). *Desecheo Isl. Puerto Rico.* Luquillo Mts. (H. Beatty); Mayagüez (A. F. Archer). *Virgin Isl.* St. Croix (Beatty; A. F. Archer); St. Thomas (many coll.); St. Johns (F. E. Lutz); Tortola (A. F. Archer). *Lesser Antilles.* Trinidad (MNHN); Los Testigos (MNHN).

Venezuela. Dist. Fed.: Caracas (E. Simon, MNHN). *Aragua:* Tovar (E. Simon, MNHN); Maracay (A. M. Nadler). *Carabobo:* San Estebán (E. Simon, MNHN). *Ecuador.* Napo-Pastaza: 3-13 km N of Puyo (E. I. Schlinger, E. S. Ross). Guayas: S of Manglaralto (E. I. Schlinger, E. S. Ross). Tungurahua: Baños (D. L., H. E. Frizzell; W. C. Macintyre). *Galapagos Isl.:* James Isl. (Templeton); Indefatigable Isl.; Floreana. *Peru. Ayacucho:* Ayacucho (W. K. Weyrauch). *Huánuco:* Divisoria, 1700 m elev. (F. Woytkowski). *San Martín:* Sapasoa, Río Huallaga (J. Ortiz de la Puente). *Arequipa:* Atiquipa, 300 m (W. K. Weyrauch). *Lima:* Lachay (P. Aquilar). *Piura:* Pariñas Valley (D. L., H. E. Frizzell); Que. Songora; Chira River (D. L., H. E. Frizzell). *Brazil. Paraíba:* Independencia (W. M. Mann). *Pernambuco:* Recife. *Rio de Janeiro:* Petropolis (H. Sick). *Minas Gerais:* Matozinhos (E. Gounelle, MNHN). *Distrito Federal:* Sumare, from *Nephila* webs, (H. Sick); Santa Teresa (H. Sick); Leblon (H. Sick). *São Paulo:* Ciudade de São Paulo (H. Sick). *Paraná:* Cubatao (MNHN). *Paraguay.* (Germain, MNHN); (Kritscher, 1957). *Alto-Parana:* Taguararapa; Apa. *Chaco:* Riacho Negro (E. Reimoser).

Argyrodes nephilae Taczanowski

Figures 133-137; Map 5

Argyrodes nephilae Taczanowski, 1872 (1873), Horae Soc. Ent. Rossicae, vol. 9, p. 114. Male and female syntypes. Male lectotype here designated from Cayenne, French Guiana, in the Polish Academy of Sciences, Warsaw, examined by Exline and Levi. O.P.-Cambridge, 1880, Proc. Zool. Soc. London, p. 324, pl. 28, figs. 4, 4a-f, specimens from the Amazon. Petrunkevitch, 1930, Trans. Connecticut Acad. Sci., vol. 30, p. 179, figs. 19-22.

Argyrodes argentata O.P.-Cambridge, 1880, *op. cit.*, p. 325. In part; specimens from the Amazon. *Not* male lectotype here designated from the East Indies, in the Hope Department of Entomology, Oxford University, examined by Levi (Figs. 148, 149).

Argyrodes cambridgei Keyserling, 1891, Die Spinnen Amerikas, Brasilianische Spinnen, p. 215. New name for *A. nephilae* O.P.-Cambridge, 1880, which Keyserling thought distinct from *A. nephilae* Taczanowski. Male lectotype here designated from the Amazon, in the Hope Department of Entomology, Oxford University, examined by Levi. Bonnet, 1955, Bibliographia Araneorum, vol. 2, pt. 1, p. 709.

Argyrodes rostratus Banks, 1908, Canadian Ent., vol. 40, p. 207, fig. 9 (upper right). Male holotype from Miami, Florida, in the Museum of Comparative Zoology, examined by Levi. Name preoccupied by *A. rostratus* Blackwall, 1877. NEW SYNONYMY.

?*Argyrodes argentatus,* F.P.-Cambridge, 1902, Biologia Centrali-Americana, Araneidea, vol. 2, p. 403, pl. 38, figs. 1, 1a (in part, probably erroneous locality, not female). Bonnet, 1955, *op. cit.*, vol. 2, pt. 1, p. 707 (American references only).

Argyrodes banksi Petrunkevitch, 1911, Bull. Amer. Mus. Nat. Hist., vol. 29, p. 166. New name for *A. rostratus* Banks, preoccupied. Bonnet, 1955, *op. cit.*, vol. 2, pt. 1, p. 709. NEW SYNONYMY.

Conopistha nephilae, Bryant, 1940, Bull. Mus. Comp. Zool., vol. 86, no. 7, p. 308.

Conopistha cambridgei, Bryant, 1942, *ibid.*, vol. 89, no. 7, p. 338, 339, figs. 21, 24.

Note. Cambridge confused several similar species when he described *A. argentata.* Specimens came from the East Indies, Ceylon, Madagascar and the Amazon. All but the East Indian specimens are females, which are difficult to place. A male is here designated as a lectotype from the East Indies (Figs. 148, 149). The females from the Amazon are most likely *A. nephilae* Taczanowski. Keyserling gave the name *A. cambridgei* to O.P.-Cambridge's description, figures and specimens, since he referred to Cambridge and did not redescribe the species or illustrate it. Although Keyserling had an additional specimen from Rio de Janeiro, the lectotype here designated is a male specimen from the Cambridge collection, which was available for study. Keyserling's own specimens from Rio de Janeiro in the British Museum (Natural History) were examined and compared to our figures by Mr. D. Clark who wrote that they are this species.

Description. Male from Florida. Carapace dusky orange-yellow. Sternum light brown. Legs pale almost white, darker at joints. Abdomen solid silver above with a narrow dark median line on dorsum and usually a small black spot at tip; venter and lower part of sides almost black with a pair of round silvery spots in front of spinnerets. Cephalic projection bearing median eyes raised. Clypeal projection slender, extending anteriorly at a slight upward angle beyond head, narrowed in middle and expanded into a knob distally (Fig. 133). Abdomen higher and proportionally heavier than in males of *A. elevatus.* Total length 2.2 mm. Carapace 1.2 mm long. First femur, 1.8 mm; patella and tibia, 1.7 mm; metatarsus, 1.4 mm; tarsus, 0.6 mm.

Female from Florida colored like male. Total length 1.7 mm. Carapace 0.7 mm long. First femur, 1.3 mm; patella and tibia, 1.3 mm; metatarsus, 0.8 mm; tarsus, 0.6 mm. Other females measured 1.7 to 3.1 mm.

Variation. Unlike *A. elevatus, A. nephilae* shows little variation. There is some individual variation in color, some specimens

being darker; all, however, are silvery. There is some variation in shape, slant and length of the male clypeal process. The genital plate of females does not appear to accumulate cuticle as the spider ages. Males vary in length from 1.7 to 2.6 mm; females 1.7 to 3.1 mm.

Diagnosis. The small size and silvery, cone-shaped abdomen (Fig. 135) separate specimens of *A. nephilae* from most *A. elevatus.* Young specimens of *A. elevatus,* however, are similar to those of *A. nephilae.* The carapace length of females in the West Indies and southeastern United States, however, does not overlap. The projections of the male carapace are of different shape (Fig. 133) and the radix (Fig. 134) is somewhat different from from that of *A. elevatus.* The epigynum is similar to that of *A. elevatus,* but is flatter and the fossae are smaller and rounder (Fig. 137). The area occupied by the seminal receptacles is only slightly narrower than that occupied by the fossae (Fig. 136).

Natural History. Petrunkevitch (1930) found specimens in Puerto Rico in the webs of *Neoscona, Nephila* and sometimes *Argiope,* but also "collected specimens in tall grass in a swamp . . . sufficient proof that the species does not necessarily construct its web in the web of large orb-weaving spiders." It has been collected from *Nephila* webs in Haiti and from *Gasteracantha* in Jamaica.

Distribution. Central and southern Florida, West Indies, to eastern South America, Galapagos Islands; Map 5.

Records. United States. Florida. Alachua Co.: Gainesville Nov. 15, 1932 (H. K. Wallace). Broward Co.: Ft. Lauderdale (M. Bates). Charlotte Co.: Murdock (A. F. Archer); Punta Gorda (S. Rounds). Dade Co.: Royal Palm Park (Blatchley); Kendall (A. M. Nadler); Tamiami Trail (F. Phillips); Miami Beach (A. L. Bacon); Miami (J. H. Bacon). Glades Co.: Palmdale. Highlands Co.: Lake Istokpoga (A. M. Nadler). Indian River Co.: Sebastian (G. Nelson); Vero Beach. Martin Co.: Indian Town (W. J. Gertsch). Monroe Co.: Tavernier (A. M. Nadler). Okeechobee Co.: Okeechobee (W. J. Gertsch). Orange Co.: Winter Park (E. M. Davis); Orlando (M. Nirenberg). Palm Beach Co.: Lake Worth. Putnam Co.: Palatka, June 12, 1935 (W. J. Gertsch). Sarasota Co.: Englewood (W. J. Gertsch); near Sarasota (W. J. Gertsch).

Bermuda. Grasmere. *West Indies. Bahama Isl.:* South Bimini (A. M. Nadler). *Cuba.* Pinar del Río: Pinar del Río. Valles: Soledad (N. Banks). Camagüey: Camagüey (Acosta). Oriente: Puerto de Bonatio (A. F. Archer); Chirivico (A. F. Archer).

Grand Cayman Isl. (R. A. Lewin). *Jamaica.* Manchester Par.: Christiana; Mandeville. St. Andrew Par.: Mona; Kingston. St. Catherine Par.: Bashy Park; Hellshire Hills; Port Henderson; Guanaboa. St. James Par.: near Great River; near Reading; Montego Bay. St. Thomas Par.: Golden Grove; Bawden; near Morant Bay. *Haiti.* Cap Haitien (J. G. Myers); Pétionville (A. F. Archer). *Dominican Republic.* near Ciudad Trujillo (A. M. Nadler); Puerto Plata (D. Hurst). *Puerto Rico.* Mayagüez (A. F. Archer); Aguadilla, Barrio Espinoc (F. Rolle); Ceiba (Serralles); Santurce (A. S. Mills). *Virgin Isl.* St. Croix (H. A. Beatty). *Martinique.* Fond la Haye (A. M. Nadler). *Santa Lucia.* Gastries (J. C. Bradley). *Colombia.* St. Andrew Isl. (H. H. Cleaves). *Venezuela. Monagas:* Caripito. *Ecuador. Guayas:* La Libertad (E. J. Schlinger, E. S. Ross). *Galapagos Isl.* Indefatigable Isl., 1935, ♀ (W. von Hagen).

Argyrodes weyrauchi new species

Figures 143-147; Map 5

Type. Male from Río Chotano, 2100 m elev., Dept. Cajamarca, Peru, June 23, 1956 (W. K. Weyrauch), in the Museum of Comparative Zoology. It is named in honor of the collector.

Description. Male carapace brown, orange anterior. Chelicerae, palpi, legs orange-yellow with tarsi darker. Sternum dark brown. Venter of abdomen, tip and longitudinal dorsal stripe nearly black, sides yellowish white with a few silvery flecks. A wide space between cephalic projection and clypeal projection. Posterior median eyes near anterior medians; both pair situated on projection (Fig. 143). Total length 3.8 mm. Carapace 2.0 mm long. First femur, 3.2 mm; patella and tibia, 3.3 mm; metatarsus, 2.5 mm; tarsus, 1.2 mm.

Female collected with male type with carapace darker and more uniform in color than male; legs pale, broadly annulated with brown. Abdomen silvery on sides, banded obliquely with dark gray. Total length 4.3 mm. Carapace 1.6 mm long. First femur, 3.1 mm; patella and tibia, 3.2 mm; metatarsus, 2.5 mm; tarsus, 1.2 mm.

Diagnosis. Argyrodes weyrauchi is quite similar to *A. elevatus*, also common in Peru. The two species, however, were not collected together, and *A. weyrauchi* can be separated by the very small radix spur (Fig. 144) and by the large circular fossae, no more than a diameter apart, of the epigynum (Fig. 147).

Natural History. The species has been collected "between leaves of Agave."

Records. Peru. Cajamarca: along Río Chotano, 2 ♂, 8 ♀ paratypes, June 23, 1956 (W. K. Weyrauch).

Argyrodes pluto Banks

Figures 138-142; Map 5

Argyrodes pluto Banks, 1906, Proc. Ent. Soc. Washington, vol. 7, p. 95. Female holotype from Falls Church, Virginia, in the Museum of Comparative Zoology, examined by Levi. The specific name is a noun in apposition, the ending is therefore unchangeable.

Conopistha ocula Muma, 1944, Amer. Mus. Novitates, no. 1257, p. 5, fig. 7. Female holotype from Salisbury, Maryland, in the American Museum of Natural History. NEW SYNONYMY.

Description. Male from Missouri with carapace, chelicerae, legs chestnut-brown with black shading. Abdomen black with a pair of silvery flecks near base and a pair of silvery streaks on each side. Cephalic projection extending forward in a nearly straight line with carapace, but quite high; clypeal projection almost vertical in front, tapering to a blunt point (Fig. 138). Abdomen higher and larger than in *A. elevatus* males and not extending as far behind spinnerets. Total length 3.7 mm. Carapace 1.8 mm long. First femur, 3.0 mm; patella and tibia, 3.3 mm; metatarsus, 2.4 mm; tarsus, 1.0 mm.

Female colored like male. Abdomen heavy with a blunt, wide tip, extending high above spinnerets, but not behind it (Fig. 140). Total length 3.9 mm. Carapace 1.8 mm long. First femur, 2.7 mm; patella and tibia, 2.8 mm; metatarsus, 2.0 mm; tarsus, 0.9 mm.

Figure 142 was prepared from the type of *A. pluto.*

Variation. Two females from the Chisos Mts. and one from Durango are paler with abdomen light brown covered with silvery flecks. The female from Chihuahua is similar but with tip of abdomen produced above and behind in a tail-like extension. Most of the Mexican male specimens have the clypeal process conspicuously shorter; in one from Chihuahua it is long and sloping as in *A. elevatus*, but it has the palpus of *A. pluto.* The genital plate of females appears variable in specimens of different ages and some appear flatter than others.

Diagnosis. Even young specimens of *A. pluto* are almost black, like the oldest females of *A. elevatus.* The carapace of the male has a different shape (Fig. 138), and the clypeal process bears regularly arranged rows of short setae. The radix of the palpus is very wide with the lateral spur arising from a swelling (Fig. 139). The embolus, with a short median spur well separated from

anterior, sickle-shaped process having distal part of seminal duct. Epigynum heavily sclerotized, rugose and black, with fossae very large (Fig. 142), separated by less than a diameter and with median rim of each opening extending forward. Seminal receptacles large, wider than long, separated by less than a radius.

Natural History. Usually only single individuals of this species are collected. It has been found in webs of *Latrodectus* (Virginia and Maryland), *Metepeira labyrinthea* (Hentz) (Maryland) and *Argiope aurantia* Lucas (Missouri).

Distribution. From Maryland, Virginia, Missouri, southwest to Chihuahua, and Jamaica; Map 5.

Records. United States. Maryland. Prince Georges Co.: Beltsville (F. R. Smith). *Virginia.* Plummer's Isl. *Missouri.* Phelps Co.: 5 mi. S of Rolla; Rolla (H. E., D. L. Frizzell). *Texas.* Brewster Co.: Chisos Mts. (W. J. Gertsch). Travis Co.: Austin (sev. coll.). *Mexico. Chihuahua:* Matachic; 13, 32 km W of Matachic (W. J. Gertsch); Primavera, 1800-2000 m elev. (W. J. Gertsch); Santa Clara Canyon (W. J. Gertsch). *Durango:* Palos Colorados, 2600 m elev. (W. J. Gertsch); Encina (W. J. Gertsch). *Tamaulipas:* Reynosa (W. Green). *West Indies. Jamaica:* Kingston, Dec. 1950 (A. Zilch, SMF).

The *A. cordillera* species group

Argyrodes cordillera (Exline), new combination

Figures 155-159; Map 6

Conopistha cordillera Exline, 1945, Ann. Ent. Soc. Amer., vol. 38, p. 516, figs. 20-23. Male holotype from Baños, Tungurahua, Ecuador, in the California Academy of Sciences.

Description. Male. Carapace, sternum brown. Legs yellow. Abdomen black with lateral stripe of silvery spots. Carapace low, with shallow groove under eyes, clypeus only slightly swollen (Fig. 155). Abdomen longer than high, extending beyond spinnerets, without humps, tip with wrinkled cuticle. Total length 3.1 mm. Carapace 1.3 mm long. First femur, 2.2 mm; patella and tibia, 2.2 mm; metatarsus, 1.7 mm; tarsus, 0.9 mm.

Female. Carapace dark gray with yellow shading anteriorly. Sternum dark brown. Legs yellowish brown. Abdomen pale above with white or silvery spots, gray to black on lower sides and venter. Clypeus low and sloping. Abdomen high extending only a little beyond spinnerets, usually with a pair of posterior lateral humps (Fig. 157). Total length 3.6 mm. Carapace 1.3 mm long. First femur, 1.9 mm; patella and tibia, 2.0 mm; metatarsus, 1.2 mm; tarsus, 0.7 mm.

Diagnosis. The male lacks projections or deep grooves on clypeus and eye region (Fig. 155). Palpus slender; embolus a straight, stiff tube; conductor nearly straight but not touching embolus; radix a flattened elongate, transparent plate lying against cymbium, dorsal to other two sclerites (Fig. 156). Epigynum slightly swollen anteriorly, lightly sclerotized; depressed in the central part near genital furrow, with a thin posterior lip and a pair of small openings at each end (Fig. 159). Seminal receptacles large, round, less than their diameter apart; connecting canals short (Fig. 158). *Argyrodes cordillera* is probably related to *A. rossi* and *A. fulvus.* Genital structures and clypeus of male are simpler than in the other two species.

Distribution. Central Ecuador; Map 6.

Records. Ecuador. Tungurahua: Baños; Ambato (H. E., D. L. Frizzell). *Azuay:* 17 km E of Paute, Feb. 17, 1955, ♀ (E. I. Sehlinger, E. S. Ross).

Argyrodes rossi new species

Figures 160-164; Map 6

Type. Male from 34 km east of Santiago, Nariño, Colombia, March 21, 1955 (E. I. Sehlinger and E. S. Ross), in the California Academy of Sciences. The species is named for Dr. E. S. Ross.

Description. Male. Carapace, sternum, palpi dark brown; legs a little lighter. Abdomen almost black, shiny with a small light patch on sides. Carapace broad at eye region. Eyes far apart, equally small, both rows very much recurved if viewed from above. Clypeus with a small projection bearing a conspicuous brush of long stiff setae; a deep but narrow cleft under projection (Fig. 160). Chelicerae unusually long and slightly diverging; fangs long. Abdomen extending far behind spinnerets (Fig. 160). Total length 4.8 mm. Carapace 1.7 mm long. First femur, 2.8 mm; patella and tibia, 3.0 mm; metatarsus, 1.5 mm; tarsus, 0.7 mm.

Female. Carapace, sternum and mouthparts dark brown. Legs orange. Abdomen pale gray with many silvery spots on dorsum. Median eyes closer to laterals than to each other. Clypeus with a groove under anterior median eyes. Chelicerae much shorter than those of male. Abdomen high with small postero-lateral humps and a conspicuous posterior protuberance (Fig. 162). Total length 4.0 mm. Carapace 1.2 mm long. First femur, 2.0 mm; patella and tibia, 2.0 mm; metatarsus, 1.1 mm; tarsus, 0.6 mm.

Diagnosis. The shape of the male clypeus and the structure of the palpus are diagnostic. The palpus has the cymbium long and narrow. The large embolus has a curved basal sclerite, and a long, corkscrew-shaped tip. The conductor is long, enclosing twisted portion of embolus. The radix is long, flat, membranous, lying against cymbium as in *A. trigonum,* but rather inconspicuous (Fig. 161). The epigynum is sclerotized and swollen, with a pair of contiguous, round fossae with a posterior rim (Fig. 164). Internally the seminal receptacles are moderately large and round. Tubes open from lateral sides of depression, make two wide spiral loops to enter receptacles laterally (Fig 163).

Records. Colombia. Nariño: 34 km E of Santiago, 1 ♀, 2 ♂ paratypes collected with type.

Argyrodes fulvus new species

Figures 165-167; Map 6

Type. Female from Rio de Janeiro, Brazil, 1890 (? E. Göldi), in the British Museum (Natural History) (no. 1890.7.1.7910-7911). The specimen had been labeled "*A. americanus* Tacz." The specific name is a Latin adjective meaning brownish yellow.

Description. Carapace, mouthparts, sternum and femora of legs brownish yellow. Distal segments of legs pale yellow with reddish brown annulations. Abdomen brownish yellow with streaks of dull silvery spots and scattered dark spots. Clypeus moderately high, nearly straight with narrow groove under eyes. Anterior median eyes large, separated by less than a diameter, nearer to anterior lateral eyes. Median ocular area nearly square. Sternum very wide in front. Abdomen high, very short, with a pair of low lateral humps and a median posterior hump (Fig. 165). Total length 2.7 mm. Carapace 1.1 mm long. First femur, 1.7 mm; patella and tibia, 1.9 mm; metatarsus, 0.8 mm; tarsus, 0.6 mm.

Diagnosis. Unlike most other species (except *A. rossi* and *A. cordillera*) the fossa of the epigynum has a posterior rim (Fig. 167). The seminal receptacles are large, sclerotized, separated by nearly a radius. The tubes are very long and narrow, of uniform diameter and following a very tortuous path, but not forming definite spirals (Fig. 166).

The *A. cancellatus* species group

Argyrodes cochleaforma (Exline), new combination

Figures 178-182; Map 6

Conopistha cochleaforma Exline, 1945, Trans. Connecticut Acad. Sci., vol. 36, p. 178, figs. 1-4. Male holotype from Baños, Tungurahua Prov., Ecuador, in the California Academy of Sciences. The specific name is a noun in apposition, and the ending is therefore unchangeable.

Description. Male. Carapace and legs yellow streaked with gray, sternum mostly gray. Abdomen with gray background, covered with silvery white patches, except for longitudinal dorsal stripe. Clypeus with a long, ventral extension (Fig. 178), both portions of the extension thickly covered with setae. Abdomen with a hump on each side and three posterior dorsal tips which are sometimes absent. Total length 3.7 mm. Carapace 1.6 mm long. First femur, 3.2 mm; patella and tibia, 3.4 mm; metatarsus, 2.3 mm; tarsus, 1.3 mm.

Female. Carapace and sternum dark brown, clypeus yellow. Legs yellow and brown annulated. Abdomen dark gray thickly covered with small silvery white spots; sometimes much lighter, nearly all silvery over a pale gray background. Abdomen very high, not extending behind spinnerets; large lateral humps, almost pointed; a median postero-dorsal protuberance bears three tips as in male (Fig. 180). Total length 2.7 mm. Carapace 1.0 mm long. First femur, 1.9 mm; patella and tibia, 1.9 mm; metatarsus, 1.3 mm; tarsus, 0.7 mm.

Diagnosis. The unique shape of the male clypeus (Fig. 178), and the two prominent teeth of the palpal radix (Fig. 179) separate this species from *A. proboscifer.* The embolus is almost hidden and the conductor very large, occupying the distal part of the palpus. The epigynum of the female has a conspicuous central projection with a round fossa on each side. The connecting canals (Fig. 181) are simple and short.

Natural History. Argyrodes cochleaforma has been found in considerable numbers in webs of *Gasteracantha* and *Argiope* together with *A. elevatus;* it was not found in the webs of *Leucauge* and *Cyclosa* of the same area (Exline, 1945).

Distribution. Ecuador and northern Peru; Map 6.

Records. (Exline, 1945). *Ecuador. Tungurahua:* near Baños, Feb. 8, 1955 (E. I. Schlinger, E. S. Ross); Baños, July 1938 (W. C. Macintyre).

Argyrodes sullana (Exline), new combination

Figures 183-187; Map 6

Conopistha sullana Exline, 1945, Trans. Connecticut Acad. Sci., vol. 36, p. 181, figs. 9-13. Male holotype from Quebrada Mogollon, Dept. Piura, Peru, in the California Academy of Sciences. The specific name is that of a town in the Chira River Valley, Peru; it is used as a noun in apposition.

Description. Male with carapace and legs yellow, sternum light brown. Abdomen light brown thickly covered on sides and lateral part of dorsum with silvery flecks. Clypeus concave beneath eyes, projecting in front of chelicerae as an upper lip; and from lower edge a longer, thinner, projection extends ventrally (Fig. 183). The opening between the projections is filled with stiff setae. The abdomen is small, high, extending a little behind spinnerets, with a pair of lateral humps. Total length 2.0 mm. Carapace 1.1 mm long. First femur, 2.2 mm; patella and tibia, 2.3 mm; metatarsus, 1.6 mm; tarsus, 0.8 mm.

Female with carapace, sternum and legs mostly yellow with some gray. Abdomen thickly covered with small silvery flecks on light gray background, posterior side a little darker and outlined with a silvery band. Clypeus with deep groove under eyes, sloping forward below. Abdomen moderately high, not extending behind spinnerets; lateral humps prominent, postero-dorsal prominence with three low, sometimes pointed tips; a pair of humps usually present on posterior side above spinnerets (Fig. 185). Total length 2.0 mm. Carapace 1.0 mm long. First femur, 1.7 mm; patella and tibia, 1.8 mm; metatarsus, 1.2 mm; tarsus, 0.6 mm.

Diagnosis. Clypeal process of male (Fig. 183) is diagnostic. Palpal radix longer than in related species, with a deep notch on anterior edge, ending medially in a single long, sharp tooth (Fig. 184); part of anterior edge heavily sclerotized. Embolus partly coiled, hidden behind radix. Conductor more heavily sclerotized than in related species, large, dissected, but not as wide as in *A. cochleaforma*. Epigynum of female raised, lightly sclerotized, with a semicircular fossa on each side having a posterior lip. There is a very small, black, projection in center (Fig. 187). Connecting canals pass posteriorly, then form an indistinct loop before entering the round seminal receptacles (Fig. 186).

Distribution. Northern Peru; Map 6.

Records. Peru. Piura: (Exline, 1945).

ARGYRODES ATOPUS Chamberlin and Ivie

Figures 188-193; Map 6

Argyrodes atopus Chamberlin and Ivie, 1936, Bull. Univ. Utah, biol. ser., vol. 3, no. 5, p. 39, pl. 9, figs. 70-72. Male holotype from Barro Colorado Island, Panama Canal Zone, in the American Museum of Natural History, examined by Exline.

Argyrodes pachysomus Chamberlin and Ivie, 1936, *ibid.*, p. 41, pl. 10, figs. 92-93. Female holotype from Barro Colorado Island, Panama Canal Zone, probably lost, examined by Exline in 1945. NEW SYNONYMY. The synonymy was first recognized by A. M. Chickering.

Description. Male. Carapace dusky gray with clypeus, mouthparts, and legs yellow. Sternum grayish yellow. Abdomen gray on dorsum, sides with a long patch of silver; a bright silver patch behind genital furrow, and a pair of patches above spinnerets; posterior tip usually dark. Carapace broad in front with widely spaced eyes. Anterior median eyes slightly larger than others, separated by nearly a diameter, a little closer to lateral eyes. Carapace illustrated by Figure 188. Abdomen high, extending a little beyond spinnerets; at widest part above spinnerets is a pair of indistinct lateral humps; tip of abdomen blunt or ending in three small humps. Total length 3.4 mm. Carapace 1.6 mm long. First femur, 2.2 mm; patella and tibia, 2.3 mm; metatarsus, 1.4 mm; tarsus, 0.8 mm. Males vary in length from 2.6 to 3.5 mm.

Female smaller and darker than male. Cephalic part of carapace narrower than in male, and eyes closer together. Chelicerae with three teeth on anterior margin, one tooth and three denticles posterior. Abdomen thicker, heavier and shorter than in male, usually with lateral humps (Fig. 190) and sometimes a tripartite posterior hump. The abdomen of gravid females is often shapeless in alcohol. Total length of female 2.4 mm. Carapace 0.8 mm long. First femur, 1.2 mm; patella and tibia, 1.2 mm; metatarsus, 0.7 mm; tarsus, 0.5 mm. Length varies from 1.8 to 2.7 mm.

Variation. Color variation is great, but silvery spots are nearly always present. The shape and humps of the abdomen are variable, especially in females. The slant of the male clypeus and the direction of its dorsal projection show some variation. In females the spacing betweeen the seminal receptacles varies from their radius to over a diameter. The connecting canals follow different paths in different individuals. A male 3.5 mm long and female 2.8 mm long from Mera, Loreto, Peru are paler and covered with silver flecks. The clypeus of the male has the upper projection shorter.

Diagnosis. *Argyrodes atopus* is similar to *A. cochleaforma, A. proboscifer* and *A. sullana.* The large U-shaped radix (Fig. 189) distinguishes the males. The swollen female genital plate with its conspicuous black tongue-like projection with indistinct openings (Fig. 193) on each side, separates the female from others except *A. cochleaforma,* in which connecting canals are much less winding.

Distribution. Panama, Venezuela to Ecuador; Map 6.

Records. Panama Canal Zone. Barro Colorado Isl. (numerous coll.); Fort Davis, 1936 (A. M. Chickering); Balboa, Aug. 1936 (A. M. Chickering). *Panama.* El Valle, July 1936 (A. M. Chickering). *Venezuela.* [probably northern Venezuela coll. by E. Simon] (MNHN). *Ecuador. Napo-Pastaza:* Mera, Feb. 12, 1955, ♀ ♂ (E. I. Schlinger, E. S. Ross).

Argyrodes proboscifer (Exline), new combination

Figures 194-198; Map 6

Conopistha proboscifera Exline, 1945, Trans. Connecticut Acad. Sci., vol. 36, p. 184, figs. 5-8. Male holotype from near Mera, Napo-Pastaza, Ecuador, in the California Academy of Sciences.

Description. Male. Carapace, sternum dark brown. Legs yellowish brown. Abdomen blackish with a longitudinal light stripe covered by large silvery areas and a few silvery spots on posterior and venter. Carapace low with a ventral clypeal projection, having a dorsal excavation near its tip (Fig. 194). Stiff setae fill the hollow. Abdomen elongated far behind and sometimes above spinnerets with a pair of postero-lateral humps, posterior tip blunt. Total length 2.9 mm. Carapace 1.3 mm long. First femur, 1.7 mm; patella and tibia, 1.9 mm; metatarsus, 1.2 mm; tarsus, 0.7 mm.

Female. Carapace and legs brownish yellow. Abdomen dark brown to black with most of sides pale with silvery spots. Abdomen much higher than that of male, extended behind and above spinnerets with postero-lateral humps more conspicuous (Fig. 196). Total length 2.6 mm. Carapace 0.8 mm long. First femur, 1.1 mm; patella and tibia, 1.2 mm; metatarsus, 0.6 mm; tarsus, 0.5 mm.

Diagnosis. The different shape of the male clypeus (Fig. 194) and abdomen separate this species from *A. cochleaforma.* The radix has an anterior heavily sclerotized truncate extension bearing three teeth in a line, the distal one being the longest. The embolus is heavy, stiff and curved. The conductor is large, mostly

membranous divided distally into two nearly equal leaf-like apophyses (Fig. 195). Epigynum (Fig. 198) large and not sclerotized, with a small very dark central protruding lip having an opening on each side. The connecting canals are very long and irregularly coiled (Fig. 197).

Natural History. The spiders were collected from *Gasteracantha* webs.

Distribution. Ecuador and northern Peru; Map 6.

Records. Ecuador. (Exline, 1945). *Peru. Junín:* near Utcuyac, Feb. 1948 (F. Woytkowski).

Argyrodes ecaudatus (Keyserling), new combination

Figures 170-172; Map 6

Faiditus ecaudatus Keyserling, 1884, Die Spinnen Amerikas, Theridiidae, pt. 1, p. 160, pl. 7, fig. 99. Female type from Uassa [Uaçá, Amapa, Brazil], in the Polish Academy of Sciences, Warsaw, examined by Levi.

Figures 170-172 were prepared from the type specimen; no other specimens were available.

Argyrodes arthuri new species

Figures 199-205; Map 7

Type. Male from Barro Colorado Island, Panama Canal Zone, Aug. 1939 (A. M. Chickering), in the Museum of Comparative Zoology. This species is named for Dr. Chickering.

Description. Male. Carapace and palpal tarsus dark brown; legs, mouthparts and sternum yellowish brown. Abdomen dark brown anteriorly on dorsum, tan with black patches and a solid black posterior tip; silvery spots and patches on sides. Eyes small with anterior median eyes larger than others and protruding from anterior edge of cephalic projection (Fig. 199). Posterior median eyes separated by more than a diameter, quite distant from laterals. Clypeus with deep median cleft behind groove. Chelicerae short with a short fang, three or four teeth on anterior margin and one tooth posterior. Abdomen cylindrical, tapering to a blunt tip; tip in a few specimens divided into a median upper and a pair of lower tubercles. Anterior part of dorsum with scutum. Total length 4.5 mm. Carapace 1.7 mm long. First femur, 3.1 mm; patella and tibia, 3.1 mm; metatarsus, 2.3 mm; tarsus, 1.0 mm. Males vary in length from 4.0 to 5.0 mm.

Female. Coloration as in male, except silvery patches on abdomen are larger and more numerous. Eyes closer together than in

male. Clypeus low, somewhat sloping and with wide, shallow groove under eyes. Abdomen shaped and patterned as in male, but without sentum (Fig. 201). There are slight lateral humps in gravid females. Total length 4.2 mm. Carapace 1.3 mm long. First femur, 2.3 mm; patella and tibia, 2.2 mm; metatarsus, 1.7 mm; tarsus, 0.8 mm. Females vary from 3.0 to 4.6 mm in length.

Diagnosis. *Argyrodes arthuri* is similar to *A. gertschi.* The carapace of the male (Fig. 199) has the anterior median eyes on the cephalic projection and the clypeus bulging below, leaving a large excavation between. The palpus (Fig. 200) has the tegulum shorter than usual. The basal coil of embolus is supported by the radix, the end by the saber-like arm of the conductor. The radix of *A. gertschi* is split almost to the base; the radix of *A. arthuri* is divided into two parts, a median selerite and a mesal selerite. The palpal femur is short with a mesal, blunt apophysis; the patella is curved. The epigynum (Figs. 203-205) has the central area swollen with a median posterior depression. The anterior half of the depression is covered by a hood that is incomplete or broken in many specimens (Figs. 203, 204). The internal genitalia (Fig. 202) are white and not sclerotized. There is a short blind sac anterior to the entrance of the duct into the anterior end of the seminal receptacles.

Distribution. Only known from Panama Canal Zone; Map 7.

Records. Panama Canal Zone. Barro Colorado Isl., June, July, Aug. 1939; July 1954, ♀ ♂ paratypes; Forest Reserve, July 1954 (all A. M. Chickering).

Argyrodes gertschi new species

Figures 206-211; Map 7

Type. Male from El Volcán, 1600 m elev., Chiriquí, Panama, Feb. 21, 1936 (W. J. Gertsch), in the American Museum of Natural History. This species is named after Dr. W. J. Gertsch.

Description. Male. Carapace, sternum, tarsus of palpus, mouthparts and base of abdomen reddish brown. Legs yellow. Most of abdomen pale gray, thickly covered with large silvery patches. Carapace rounded in front. Eyes nearly equal in size. Anterior median eyes their diameter apart, slightly more than their diameter from laterals. Posterior median eyes two diameters apart. Clypeus sloping forward and partially divided under the deep groove (Fig. 206). Clypeus narrows above chelicerae to a blunt point. Chelicerae and legs short. Abdomen extended far behind spinnerets, tapering to blunt wrinkled tip. Proximal end

of abdomen with a large dorsal sclerotized shield. Total length 4.3 mm. Carapace 1.5 mm long. First femur, 2.1 mm; patella and tibia, 2.3 mm; metatarsus, 1.6 mm; tarsus, 0.7 mm.

Female. Paler than male, mostly pale yellow with carapace infused with gray. Clypeus low, slightly slanting, and divided by shallow groove. Abdomen without scutum, elongate as in male, but extending behind spinnerets, with a low pair of lateral humps; posterior tip divided into one upper and two lower points (Fig. 208). Total length 3.5 mm. Carapace 1.1 mm long. First femur, 1.5 mm; patella and tibia, 1.6 mm; metatarsus, 1.0 mm; tarsus, 0.6 mm. A second specimen, total length, 2.9 mm; a third damaged, but about 4.5 mm long.

Diagnosis. Argyrodes gertschi is similar to *A. arthuri,* but can be distinguished by the shape of the male clypeus (Fig. 206). The radix of the palpus of *A. gertschi* is split longitudinally nearly to its base, that of *A. arthuri* is split into two sclerites. The small, heavy embolus is only partially coiled (Fig. 207). The epigynum is similar to that of *A. atopus,* with a pointed beak and openings immediately posterior (Figs. 210-211). Internal structure is as in *A. arthuri,* with a pair of very large, pale but well sclerotized, contiguous seminal receptacles. The tubes enter anteriorly and lie medially and ventrally to the receptacles (Fig. 209).

Distribution. Only known from northern Panama; Map 7.

Records. Panama. Chiriquí: El Volcán, 1600 m elev., ♂ 3 ♀ paratypes collected with type.

Argyrodes altus Keyserling

Figures 212-216; Map 7

Argyrodes altus Keyserling, 1891, Die Spinnen Amerikas, Brasilianische Spinnen, p. 211, pl. 8, fig. 152. Female type from Espírito Santo, Brazil, in the British Museum (Natural History), examined by Levi. Göldi, 1892, Mitt. Osterlande, neue Folge, vol. 5, p. 224, 228.

Conopistha pozonae Schenkel, 1953, Verhandl. Naturf. Gesell. Basel, vol. 64, no. 1, p. 11. Female type from El Pozon, Dto. Acosta, Prov. Falcon, Venezuela, in the Naturhistorisches Museum, Basel, examined by Levi. NEW SYNONYMY.

Description. Male from Venezuela. Carapace, sternum, distal segments of legs and tarsi of palpi orange-brown infused with gray. Clypeus, mouthparts, femora of legs and proximal segments of palpi clear yellowish orange. Abdomen light brown with a black patch on basal part of dorsum, and entire tip black infused with brown. A patch of silvery spots on each side near

base, another across center part of dorsum, and an oblique line on posterior lateral margin. Carapace slender. Clypeus very high, slanting forward beneath eyes to closed groove; swollen and projecting below and hanging over base of chelicerae (Fig. 212). Anterior median eyes a little larger than others, less than a diameter apart, about same diameter from posterior medians and farther from laterals. Ocular area wider behind than in front. Abdomen extending far behind spinnerets, somewhat enlarged at posterior end and bluntly rounded with a trace of paired lateral humps. Cuticle of posterior part of abdomen wrinkled. Total length 3.1 mm. Carapace 1.4 mm long. First femur, 2.1 mm; patella and tibia, 2.3 mm; metatarsus, 1.6 mm; tarsus, 0.6 mm.

Female from Venezuela. Paler than male; carapace orange-yellow infused with gray; sternum and proximal part of femora pale yellow; distal segments of legs grayish orange. Abdomen with dorsum with broad, longitudinal, light brown band. Sides, posterior, and venter thickly covered with silvery flecks. A brown band including some dark gray on each side above spinnerets and a gray streak along each lateral posterior margin. Carapace shorter and broader than in male. Clypeus sloping forward, rounded, without groove. Eyes similar to those of male. Abdomen slender, extended above rather than behind spinnerets, distal end blunt, with a trace of lateral humps as in male (Fig. 214). Cuticle of posterior side wrinkled. Total length 2.2 mm. Carapace 1.0 mm long. First femur, 1.6 mm; patella and tibia, 1.5 mm; metatarsus, 0.7 mm; tarsus, 0.5 mm.

Diagnosis. The male *A. altus* can be distinguished from most species by the high, bulging clypeus (Fig. 212), similar to that of *A. amplifrons,* and from the latter by the small, heavily sclerotized, crescent-shaped palpal radix (Fig. 213). The conductor lies within the tip of the cymbium; a posterior projection of the conductor interlocks with the radix. The embolus forms a small heavy spiral, not visible in ventral view, hidden behind radix and projection of conductor. The epigynum is very large, central area concave with sclerotized wall. Openings large, anterior to a pair of oblique median ridges (Fig. 216). Tubes are unusually wide with membranous walls, nearly encircling the seminal receptacles, narrowing toward receptacles. Receptacles separated by a radius, heavily sclerotized (Fig. 215). No other species has a similar epigynum.

Natural History. Göldi (1892), who collected this species for Keyserling, reports finding the spider in virgin tropical forest

within several days' trip from São Eduardo [Santo Eduardo] on the Rio Itabapoana, the border river between the provinces Rio de Janeiro and Espírito Santo.

Distribution. Venezuela to southern Brazil; Map 7.

Records. Venezuela. Carabobo: San Estebán, Jan., Feb. 1888, ♀ ♂ (E. Simon, MNHN).

Argyrodes amplifrons O.P.-Cambridge

Figures 217-224; Map 7

Argyrodes obtusa O.P.-Cambridge, 1880, Proc. Zool. Soc. London, p. 338, pl. 30, fig. 17. Male holotype from the Amazons, [Brazil], in the Hope Department of Entomology, Oxford University, examined by Levi. Simon, 1894, Histoire Naturelle des Araignées, vol. 1, p. 496, fig. 505. NEW SYNONYMY.

Argyrodes amplifrons O.P.-Cambridge, 1880, *ibid.*, p. 339, pl. 30, fig. 17. Male and female syntypes from the Amazons, [Brazil], in the Hope Department of Entomology, Oxford University, examined by Levi. Keyserling, 1884, Die Spinnen Amerikas, Theridiidae, pt. 1, p. 186, pl. 9, fig. 111; 1891, *op. cit.*, Brasilianische Spinnen, p. 214, pl. 8, fig. 156. Simon, 1894, *op. cit.*, p. 499.

Conopistha pizai Soares and Camargo, 1948, Bol. Mus. Paraense, vol. 10, p. 364, fig. 14, ♂. ? Juv. male type from Chavantina, Mato Grosso, Brazil, in the Departamento de Zoologia Secretaria da Agricultura do Estado de São Paulo. NEW SYNONYMY.

Note. Because specimens belonging to this species have been correctly named *A. amplifrons,* and the name *A. obtusus* has been incorrectly used for several other species, we prefer to use the name *A. amplifrons* even though *A. obtusus* has page priority. *Argyrodes obtusus* of F.P.-Cambridge 1902 is *A. subdolus; A. obtusus* of Petrunkevitch 1930 is *A. exiguus.* Specimens of several species from the West Indies, Guatemala, and Mexico have been erroneously identified as *A. obtusus* in collections.

Description. Male from San Martín, Peru. Carapace and legs chestnut brown, sternum and tarsi of palpi darker. Abdomen brown with large pale patches, flecked with silver. Carapace flat, broad and rounded in front. Anterior median eyes slightly protruding over clypeus. Clypeus with cleft near anterior median eyes; below cleft a large, divided bulge overhangs chelicerae (Fig. 217). Palpi very short with large tarsi. Base of abdomen with large sclerotized area. Abdomen extending far behind and above spinnerets, tapering posteriorly, with tip distinctly bifid. Total length 4.6 mm. Carapace 1.6 mm long. First femur, 3.3 mm; patella and tibia, 3.3 mm; metatarsus, 2.3 mm; tarsus, 1.0 mm.

Female from Huánuco, Peru. Carapace and legs yellow with gray infusions, sternum pale yellow. Abdomen white covered with silvery patches, with a broad gray longitudinal band on dorsum. Abdomen very high above spinnerets, and extending only a little behind them, blunt and bifid (Fig. 221). Total length 2.3 mm. Carapace 0.9 mm long.

Figures 217, 218, 221, 222, 224 were prepared from the syntypes of *A. amplifrons*.

Variation. Color, shape of abdomen, and length of male clypeal protrusion vary within populations. There is considerable variation in shape of genitalia (Figs. 218-220, 222, 223) between different populations. A male from Paraguay, 3.0 mm long, has carapace, legs and sternum yellow with gray infusions. Abdomen very pale yellow, flecked with silver and gray infusions ventrally. Abdomen low, with a suggestion of lateral humps near tip; tip very blunt, not bifid but with cuticle wrinkled in a pair of concentric circles. A male 3.7 mm long, much as above, but carapace, legs and sternum orange.

Males from Panama range from 2.7 to 3.3 mm total length. Cephalothorax pale yellow to dark brown, abdomen varies from almost white with dark gray to dark gray or brown. None has the tip of the abdomen bifid or trifid. The palpal radix is more concave anteriorly, and has a mesal tooth; the conductor is slightly different in shape (Fig. 220). Two females collected in Panama measure 2.8 mm and 3.0 mm long. Both are very pale, with the abdomen silver flecked, high, and bifid at tip. The epigyna are more transparent, and the median ridge more distinct. The connecting canals of all females examined appear to be larger in diameter than in the female type (Fig. 222), and the seminal receptacles are smaller (Fig. 223).

Diagnosis. The bulbous clypeus (Fig. 217) is diagnostic in the male; *A. altus* also has a swollen clypeus but differs in shape of the palpal radix (Figs. 218-220). Bulb of palpus with parts tightly fitting; tegulum with two distinct concentric loops of duct; median apophysis large showing duct; subtegulum with large tooth extending over median apophysis on mesal side (not visible in figures); radix short, wide, narrowing to ectally directed point; embolus heavy, hidden, forming small coil firmly supported by radix and visible only through it; conductor large, sclerotized, dissected, supporting embolus, with a large, distally attached apophysis that lies ventrally and bisects tip of bulb, almost reaching radix posteriorly (Figs. 218-220). The female differs from other species by being pale, with abdomen bifid at

tip, and by having epigynum large, poorly sclerotized. Epigynum with a pair of uniquely wide, curved ridges uniting medially in a scape with openings inside posterior ends of ridges (Fig. 224). Connecting canals large, forming two large loops, then narrowing to enter seminal receptacles. Seminal receptacles are anterior to ridge (Figs. 222, 223).

Distribution. Rare in Panama, to Paraguay, most collections from interior of South America; Map 7.

Records. Panama Canal Zone. Barro Colorado Isl., ♀ ♂ (A. M. Chickering); ♂ (T. C. Schneirla). *Peru. Loreto:* (Keyserling, 1884); Pebas, ♀ (M. de Mathan, MNHN). *San Martín:* 20 km NE of Moyobamba, 1600 m elev., 2 ♂ (F. Woytkowski). *Huánuco:* Divisoria, ♀ (F. Woytkowski). *Brazil. Pará:* Santarém (BMNH). *Rio de Janeiro:* (Keyserling, 1891). *Santa Catarina:* Nova Teutonia, ♀ ♂ (F. Plaumann, SMF). *Paraguay.* Apa, ♂. *Bolivia. Cochabamba:* Esperítu Santo (MNHN).

Argyrodes acuminatus Keyserling

Figures 225-230; Map 7

Argyrodes acuminatus Keyserling, 1891, Die Spinnen Amerikas, Brasilianische Spinnen, p. 207, pl. 7, fig. 149. Male, female syntypes from Serra Vermella [Serra Vermelha, right bank of Río Paraiba, probably near São Fidélis, Rio de Janeiro], Miracena [Minas Gerais], Facenda Calvario [near São Fidélis, left bank of Río Paraiba, Rio de Janeiro], Espírito Santo, Brazil, in the British Museum (Natural History), examined by Levi. Göldi, 1892, Mitt. Osterlande, neue Folge, vol. 5, p. 224.

Göldi collected this species in several localities, all from virgin forests in hot lowlands; no additional specimens were available. The illustrations were prepared from the syntypes.

Argyrodes exiguus new species

Figures 231-235; Map 7

Argyrodes obtusus, Petrunkevitch, 1930, Trans. Connecticut Acad. Sci., vol. 30, p. 186, figs. 29-32. Not *A. obtusus* O.P.-Cambridge.

Type. Male from Collazo, east of San Sebastián, Puerto Rico, July 30, 1958 (A. F. Archer), in the American Museum of Natural History. The specific name is an adjective meaning small.

Remarks. Petrunkevitch's figures show the carapace, and the palpus from a lateral angle, seemingly cleared, and perhaps without radix. His specimen was examined by Exline; it is not well pigmented and is a little smaller than others.

Description. Male type. Carapace, sternum and legs dusky yellow, streaked. Mouthparts and proximal parts of legs yellow. Abdomen yellow; dorsum at base and entire posterior third black; two pairs of irregular silvery stripes on sides, three pairs of small silver spots on posterior; venter reddish without silver. Anterior median eyes slightly larger than others, not quite a diameter apart, a little farther from laterals. Posterior median eyes separated by two diameters, closer to laterals. Clypeus high, with closed groove below eyes, notched and swollen below groove, almost straight below swelling to edge (Fig. 231). Legs slender; sternum wide in front. Abdomen elevated far above spinnerets and blunt tip extending posteriorly beyond them. A pair of very low lateral humps above spinnerets. Total length 2.6 mm. Carapace 1.0 mm long. First femur, 1.3 mm; patella and tibia, 1.6 mm; metatarsus, 1.0 mm; tarsus, 0.7 mm.

Female from Cuba. Carapace dusky yellow. Mouthparts yellow with gray markings. Sternum gray. Legs pale yellow annulated and streaked with reddish brown and gray. Abdomen dark gray with a pair of silvery spots at base of dorsum, two pairs of large silvery spots and one very small pair posterior; a cluster of silvery spots on each lateral hump, on venter, and a few scattered on dorsum. Carapace short and wide. Clypeus only moderately high with groove under eyes. Anterior median eyes slightly larger than others, separated by about a diameter. Median ocular area square, close to lateral eyes. Sternum unusually wide in front. Abdomen projecting above and a little beyond spinnerets, with a low hump above spinnerets and a blunt posterior dorsal hump (Fig. 233). Total length 2.2 mm. Carapace 0.8 mm long. First femur, 0.9 mm; patella and tibia, 1.1 mm; metatarsus, 0.6 mm; tarsus, 0.5 mm.

Diagnosis. The form of the male clypeus (Fig. 231) separates this from males of other West Indian species. The palpal radix is diagnostic, large and high, with a large spur in center of anterior edge. The embolus is thick, forming a wide spiral. The conductor is large with a tooth extending slightly beyond cymbium (Fig. 232). The epigynum of the female has a wide, fairly long fossa, an anterior cuticular rim, with central thickened lip, continuous around lateral margins. A conspicuous brown spot marks the center of each side of fossa (Fig. 235). The seminal receptacles are small. Large tubes diminishing in diameter from openings to receptacles follow an S-shaped path (Fig. 234). Males and females have not been collected together and it is therefore not certain that they belong together.

Distribution. Cuba, Puerto Rico; Map 7.

Records. Cuba. Pinar del Río: N of Vinales, Sept. 16-22, 1913, ♀. *Puerto Rico.* Martín Peña, Nov. 7, 1925, ♂ (A. Petrunkevitch); Estación Experimental, Mayagüez, Aug. 1958, ♂ (A. F. Archer).

Argyrodes plaumanni new species

Figures 168, 169; Map 9

Type. Male from Nova Teutonia, lat 27°11′, long 52°23′, Santa Catarina, Brazil, 1930-1940 (F. Plaumann), in the Senckenberg Museum, Frankfurt. The species is named for the collector.

Description. Carapace brown paling to brownish yellow in eye region and on clypeus. Tarsi of palpi, sternum and mouthparts brown. Legs dusky orange. Abdomen with brown sclerotized basal area on dorsum and venter anterior to genital groove, otherwise grayish white covered with dull silvery flecks. Carapace short, wide and high, sloping gradually from posterior to eyes. Eye region flattened with anterior median eyes borne on pointed projection. Clypeus high, with wide, open groove separating cephalic projection from long, thumb-like clypeal projection; clypeus sloping slightly forward below (Fig. 168). Eyes small, anterior medians largest, separated by a diameter, and about a diameter and a half from posterior medians, much farther from anterior laterals. Posterior eyes equally spaced, about four diameters apart. Abdomen extending far behind spinnerets with a pair of dorso-lateral humps midway between spinnerets and posterior bifurcate tip (Fig. 168). Total length 4.5 mm. Carapace 1.6 mm long. First femur, 2.7 mm; other segments missing.

Diagnosis. Shape of clypeus and cephalic region (Fig. 168) is diagnostic and similar to that of *A. argyrodes* group. The palpal structure and shape of the abdomen relate it to *A. cancellatus.* Palpus wide; radix large with transverse anterior margin ending in sharp ventrally bent tooth. Embolus narrow, forming wide spiral, seen only through radix. Conductor conspicuous with rounded basal portion, bearing a pair of scissor-like blades that protrude beyond cymbium (Fig. 169). The female is unknown.

Argyrodes woytkowskii new species

Figures 173-177; Map 9

Type. Male from Utcuyacu, Junín, Peru, 1600-2200 m elev., March 1948 (F. Woytkowski), in the American Museum of Natural History. The species is named for the collector, who has

contributed greatly in exploring the flora and fauna of Peru.

Description. Male. Carapace and chelicerae brown. Sternum, labium and palpal tarsi almost black. Legs brownish yellow. Abdomen black infused with yellow anteriorly, with a wide saddle of pale yellow flecked with silvery spots in posterior half. A pair of silvery spots behind and above spinnerets, and three silvery spots at posterior extremity. Another male is slightly lighter. Cephalic part of carapace elevated gradually from thoracic groove. Clypeus high, sloping forward beneath anterior median eyes to a deep groove containing a brush of stiff setae; ventral part bulging (Fig. 173). Anterior median eyes large, separated by only slightly more than a radius. Posterior median eyes smaller, separated by two diameters. Abdomen bluntly rounded behind spinnerets. The cuticle of the posterior tip somewhat wrinkled. Total length 2.6 mm. Carapace 1.2 mm long. First femur, 2.5 mm; patella and tibia, 2.7 mm; metatarsus, 1.9 mm; tarsus, 1.1 mm.

Female. Carapace and chelicerae brownish yellow infused with dark gray. Legs bright yellow. Sternum dark gray. Abdomen as in male with pale saddle larger and covering more of sides, and a pair of silvery spots in front of spinnerets as well as the pair behind. Posterior side mostly pale. Cephalic part of carapace not elevated as in male. Clypeus moderately high with deep groove under eyes, somewhat bulging and sloping. Eyes as in male. Abdomen with very slight posterior hump (Fig. 175). Total length 2.0 mm. Carapace 0.8 mm long. First femur, 1.3 mm; patella and tibia, 1.4 mm; metatarsus, 0.7 mm; tarsus, 0.6 mm.

Diagnosis. Argyrodes woytkowskii has a narrow radix, projecting on venter with a long spine, and two distal teeth (Fig. 174); it does not support the embolus. The short, heavy embolus forms a semicircle. The conductor lies entirely within the cymbium of the bulb. The epigynum is very wide and has round openings at lateral ends of a wide, sclerotized groove (Fig. 177). From the openings the tubes pass toward the median line, fold back in an arched curve to enter the seminal receptacles. Receptacles separated by a radius (Fig. 176).

Records. Peru. Junín: Uteuyacu, 1600-2000 m elev., Feb. 8-26, 1948, 1 ♀, 1 ♂ paratypes (F. Woytkowski).

Argyrodes americanus (Taczanowski)

Figures 236-247; Map 8

Ero americana Taczanowski, 1872 (1873), Horae Soc. Ent. Rossicae, vol. 10, p. 62. Female lectotype here designated from Uassa, French Guiana [Rio Uaçá, Amapa, Brazil], in the Polish Academy of Sciences, Warsaw, examined by Levi.

Argyrodes trituberculatus Becker, 1879, Ann. Soc. Ent. Belgique, vol. 22, p. 79, pl. 1, figs. 1-3. Male type from Pascagoula, Mississippi, in the Institut Royal des Sciences Naturelles de Belgique, Brussels, examined by Levi. Keyserling, 1884, Die Spinnen Amerikas, Theridiidae, pt. 1, p. 203, pl. 10, fig. 122. Simon, 1894, Histoire Naturelle des Araignées, vol. 1, p. 499. NEW SYNONYMY.

Argyrodes americanus, Keyserling, 1884, Die Spinnen Amerikas, *op. cit.*, Theridiidae, pt. 1, p. 195, pl. 9, fig. 117; 1891, *op. cit.*, Brasilianische Spinnen, p. 215. F.P.-Cambridge, 1902, Biologia Centrali-Americana, Araneidea, vol. 2, p. 403, pl. 38, figs. 4, 5. Petrunkevitch, 1930, Trans. Connecticut Acad. Sci., vol. 30, p. 185, figs. 27, 28. Bryant, 1940, Bull. Mus. Comp. Zool., vol. 86, no. 7, p. 306. Bonnet, 1955, Bibliographia Araneorum, vol. 2, pt. 1, p. 706.

Argyrodes ululabilis Keyserling, 1891, *op. cit.*, Brasilianische Spinnen, p. 212, pl. 8, fig. 153. Female type from Taquara do Mundo Nova, Rio Grande do Sul, Brazil, in the British Museum (Natural History), examined by Levi. NEW SYNONYMY.

Argyrodes argenteola O.P.-Cambridge, 1894, Biologia Centrali-Americana, Araneidea, vol. 1, p. 128, pl. 16, fig. 4. Male type from Teapa, Tabasco, [Mexico], in the British Museum (Natural History), examined by Levi. Bonnet, 1955, *op. cit.*, p. 707.

Argyrodes aurea O.P.-Cambridge, 1896, *op. cit.*, p. 207, pl. 26, fig. 1; 1898, p. 259, pl. 38, fig. 4. Female type from Teapa, Tabasco, [Mexico], in the British Museum (Natural History), examined by Levi.

Argyrodes parvior Chamberlin and Ivie, 1936, Bull. Univ. Utah, biol. ser., vol. 3, no. 5, p. 37, pl. 9, figs. 68, 69. Male type from Panama Canal Zone, in the American Museum of Natural History, examined by Exline. (Not female, pl. 10, figs. 85-87 = *A. caudatus*.) NEW SYNONYMY.

Argyrodes indignus Chamberlin and Ivie, 1936, *ibid.*, p. 38, pl. 10, figs. 94, 95. Female type from Panama Canal Zone, lost. NEW SYNONYMY.

Description. Male from Panama. Carapace and mouthparts brownish yellow. Legs brownish orange with proximal parts of femora yellow. Sternum orange-brown. Abdomen gray with basal part and spinnerets brown, dark gray in patches on humps, and with scattered bright silver spots or patches. A pair of round silver spots above spinnerets, none on venter. Carapace with cephalic part low. Clypeus low with closed groove under eyes, nearly straight, slightly projecting ventrally in midline (Fig. 242). Anterior median eyes larger than others, separated by

about a diameter, farther from laterals. Posterior median eyes nearer posterior laterals than each other. Abdomen highest and widest above spinnerets with a pair of lateral humps; posterior part rounded, extending beyond spinnerets with a median posterior hump (Fig. 243). Total length 3.5 mm. Carapace 1.6 mm long. First femur, 3.4 mm; patella and tibia, 3.3 mm; metatarsus, 1.9 mm; tarsus, 0.8 mm.

Female. Carapace, mouthparts and distal parts of femora, tibiae and tarsi yellowish brown. Proximal parts of femora, patellae and metatarsi yellow. Abdomen mostly mottled silver with dark gray patch anterior and streaks of dark gray medially on dorsum and on posterior side. Spinnerets and venter anterior to genital groove brown. A pair of round silver patches above spinnerets, as in male. Carapace similar to that of male with clypeus nearly as high. Eyes as in male except medians nearer laterals. Dorsum of abdomen with lateral humps above spinnerets more conspicuous than in male; the single low posterior hump as in male (Fig. 244). Two silver spots above spinnerets are often borne on small raised protuberances. Total length 2.9 mm. Carapace 1.2 mm long. First femur, 1.8 mm; patella and tibia, 1.8 mm; metatarsus, 0.9 mm; tarsus, 0.5 mm.

Variation. Panamanian males vary from 2.3 mm in length to 3.5 mm; females from 2.0 to 3.2 mm. Specimens from other regions are within this size range, those from Florida and the West Indies usually being small, and those from southern Mexico, Costa Rica and Brazil usually large. The female abdomen varies greatly in width (from 1.0 to 3.5 mm) becoming much wider as the ovaries develop. The male abdomen is not as variable, but the humps of some males are reduced, and old specimens appear to lose the humps and the posterior part of the abdomen becomes low and blunt.

Color and pattern are variable in any series of specimens, even from one locality. Specimens with carapace and legs pale yellow and abdomen mostly silver are found in association with dark specimens (carapace and legs brown, abdomen nearly black with bright lateral silver patches). When the female abdomen is very wide and high, the color is usually pale, thickly mottled with tiny silver spots.

The genitalia are not as variable as in most widespread species, but a difference in the amount of sclerotization of parts of the male palpus changes the appearance somewhat. The radix is often quite transparent, and sometimes dark and well outlined. The conductor appears entirely fleshy and almost formless in some palpi, and in others shows some sclerotization (Figs. 236-241).

The seminal receptacles are oval to almost spherical (Figs. 245, 246). South American females usually seem to have the ducts longer.

Figures 240, 241 were prepared from the type of *A. trituberculatus.*

Diagnosis. Many individuals can be separated from *A. globosus* by the posterior median hump on the abdomen, but this is sometimes absent. Others can be separated by the epigynum (Fig. 247). The palpi seem alike superficially, but when cleared in oil, *A. americanus* is seen to have the embolus much shorter than has *A. globosus,* and usually lying near the anterior edge of the radix (Figs. 236, 238, 240). The female connecting ducts are shorter than in *A. globosus,* the seminal receptacles oval, usually less than their radius apart and larger (0.08 to 0.09 mm the shorter diameter), while those of *A. globosus* are spherical, usually their radius or more apart and are smaller, 0.07 mm in diameter.

In the West Indies and Panama, *A. americanus* has been confused with small specimens of *A. caudatus,* and in Florida with *A. cancellatus.* The shape of the radix separates males, and the wide fossae in the epigyna of the latter two species separate females.

Females of *A. atopus* can be confused with *A. americanus* in Panama. Internally the structure of the epigyna is very different. Also, the abdomen of *A. atopus* bears a pair of bright silver markings in front of the spinnerets; *A. americanus* has no such silver markings on the venter, but a pair behind the spinnerets on the posterior side.

Distribution. Southeastern United States, Mexico, Central America, West Indies, Peru to southern Brazil; Map 8.

Records. United States. Florida. Alachua Co.: Gainesville (H. K. Wallace; W. J. Gertsch); Newnans Lake. Highlands Co.: Lake Placid (M. Cazier). Indian River Co.: Sebastian (G. Nelson). Martin Co.: Port Mayaca (W. J. Gertsch, R. Forster). Sarasota Co.: Myakka River State Park (W. J. Gertsch). *Texas.* Cameron Co.: (L. I. Davis); Olmito. Hidalgo Co.: Weslaco (S. Mulaik). *Mexico. Tamaulipas:* Tampico; 10 km E of Villa Juárez [Mante] (L. I. Davis). *San Luis Potosí:* Valles (L. Steude). *Veracruz:* Veracruz (H. Wagner). *Chiapas:* Cacahuatán (C. Goodnight); Tapachula (A. Petrunkevitch); La Zacualpa (A. Petrunkevitch). *Costa Rica.* Río Anonos (Tristan). *Panama.* Boquete; El Valle (both A. M. Chickering). *Canal Zone:* Barro Colorado Isl. (many coll.); Fort Randolph; Madden Dam; Miraflores Dock; Pedro Miguel (all A. M. Chickering).

Cuba. Oriente: Yunque de Baracoa (P. J. Darlington); Soledad (sev. coll.); Cuabitas (P. Alayo). *Jamaica.* St. Catharine Par.; St. James Par.; St. Andrew Par.; St. Ann Par. (A. M. Chickering); Trelawny Par. (E. Williams). *Dominican Republic.* Rain forest near Valle Nuevo (P. J. Darlington). *Peru. Cajamarca:* Bellavista, Prov. Jaen (D. L. Frizzell). *Brazil. ?Pará:* Rio Maputra [? Mapuera], 16 km S of Equator (W. G. Hassler). *Minas Gerais:* Matozinhos (E. Gounelle, MNHN). *Rio de Janeiro:* Rio de Janeiro (Keyserling coll., BMNH).

Argyrodes globosus Keyserling

Figures 248-260; Map 8

Argyrodes globosus Keyserling, 1884, Die Spinnen Amerikas, Theridiidae, pt. 1, p. 204, pl. 10, fig. 123. Male type from Crescent City, Florida, in the United States National Museum, examined by Levi.

Argyrodes argentcomaculata O.P.-Cambridge, 1896, Biologia Centrali-Americana, Araneidea, vol. 1, p. 193, pl. 24, fig. 6. Male type from Teapa, Tabasco, Mexico, in the British Museum (Natural History), examined by Levi. F.P.-Cambridge, 1902, Biologia Centrali-Americana, Araneidea, vol. 2, p. 404, pl. 38, fig. 6. NEW SYNONYMY.

Conopistha rorerae Exline, 1945, Ann. Ent. Soc. Amer., vol. 38, p. 519, figs. 38-42 (fig. 39 inaccurate). Male type from Milagro, Guayas, Ecuador, in the California Academy of Sciences. NEW SYNONYMY.

Description. Male from Florida. Carapace, mouthparts, legs mostly bright yellow to orange. Cymbium of palpus, distal segments of anterior legs reddish brown. Sternum dusky. Abdomen pale with large reddish brown markings, a large bright silver patch on each side and a pair of round silver markings above spinnerets. Venter dusky. Carapace and clypeus (Fig. 254) nearly as in *A. americanus.* Eyes nearly equal in size and more evenly spaced than in *A. americanus.* Abdomen a little longer than wide, rounded behind, without median posterior hump (Fig. 255). Total length 2.3 mm. Carapace 1.1 mm long. First femur, 1.9 mm; patella and tibia, 1.9 mm; metatarsus, 1.2 mm; tarsus, 0.6 mm.

Female from same collection as male. Carapace, mouthparts and legs mostly yellow, paler than in male, distal segments of anterior legs reddish brown. Sternum dusky yellow. Abdomen entirely mottled silver. Carapace and height of clypeus as in male. Anterior median eyes larger than others, and nearer laterals than in male. Abdomen a little longer than wide, higher than long, with a pair of angular dorsal shoulders (Figs. 256, 257). Total length 2.3 mm. Carapace 1.0 mm long. First femur, 1.6 mm; patella and tibia, 1.6 mm; metatarsus, 0.8 mm; tarsus, 0.5 mm.

Variation. Not so variable in size as *A. americanus.* Florida males measure from 1.9 to 2.8 mm in length; females from 2.1 to 2.6 mm. Color not so variable as in *A. americanus.* Some males have the abdomen mostly gray with a large bright silver patch on each side. Female abdomens vary in brightness and some have a yellow cast; some are banded with pale gray or light brown. Some Mexican males are more brightly colored than any in Florida, with deep reddish brown contrasting with the shiny silver patches.

The shape of the abdomen in both sexes is quite variable, and it may be shrivelled in alcohol. In some males the abdomen is almost bluntly angular behind but never pointed or with humps. As eggs develop in the ovary, the female abdomen increases in size and becomes rounder.

There is considerable variation in shape of the palpal radix (Figs. 248-253). Also, the diagnostic characters vary. The seminal receptacles are a radius to a diameter apart and the ducts in some individuals are much shorter (Figs. 258, 259). There seems to be a corresponding variation in length of embolus (Figs. 248, 250, 252). Several collections from near Tamazunchale have the ducts and emboli noticeably shorter (Figs. 250, 258). Whether these might be hybrids is impossible to say.

Diagnosis. Superficially most specimens can be separated from *A. americanus* by the lack of a median posterior abdominal hump. Males have the embolus noticeably longer than have *A. americanus* males (to examine the palpi, one must clear them in clove oil, and take care to tilt them correctly; Figs. 248, 250, 252). The epigynum (Fig. 260) separates some females. The seminal receptacles of *A. globosus* females are spherical and their radius or more apart (Figs. 258, 259); those of *A. americanus* are usually ovoid and are separated by less than their radius. The female ducts are longer than in *A. americanus.* The diameter of seminal receptacles is 0.7 mm with little size variation; the shorter diameter of those of *A. americanus* is between 0.8-0.9 mm.

Natural History. In Ecuador this species was taken from the webs of large orb-weavers other than *Nephila.* In Louisiana a pair of *A. globosus* was found, along with a pair of *A. cancellatus,* in the web of a female *Nephila clavipes* (Linnaeus).

Distribution. Southeastern United States, Mexico, Ecuador: Map 8.

Records. United States. South Carolina. Charleston. *Georgia.* Billy's Isl., Okefinokee Swamp. *Florida.* Alachua Co.: Gainesville (W. J. Gertsch; S. Jones). Dade Co.: Royal Palm Park

[Everglades Natl. Park] (W. S. Blatchley). Glades Co.: 5 mi. S of Lake Istopoka (A. M. Nadler); Palmdale; Archibald Biol. Sta. Highland Co.: Highland Hammock, near Sebring (W. J. Gertsch, R. Forster). Lake Co.: 7 mi. E of Apopka (M. Nirenberg); Winter Park (W. J. Gertsch). Orange Co.: Orlando (M. Nirenberg). Putnam Co.: Florahome (Leonard). St. Johns Co.: St. Augustine (R. V. Chamberlin). *Alabama.* Houston Co.: Chattahoochee State Park; Dothan; S of Dothan; Big Creek near Dothan (all A. F. Archer). *Louisiana.* St. Tammany Par.: Covington (N. Banks). *Texas.* Tyler Co.: Woodville (L. I. Davis). *Mexico. San Luis Potosí:* 8 km N of Tamazunchale (A. M., L. I. Davis); Tamazunchale (W. J. Gertsch); 11 km E of Ciudad des Maíz (A. M. Davis). *Veracruz:* Conejo (V. Roth, W. J. Gertsch); Pánuco (A. M., L. I. Davis); Tlapacoyan (H. Wagner). *Tabasco:* Teapa (C., M. Goodnight). *Chiapas:* La Zaeualpa (A. Petrunkevitch); Tapachula (A. Petrunkevitch). *Campeche:* Lerma (C., M. Goodnight). *Cuba.* Santiago, Oriente (A. F. Archer, P. Alayo). *Ecuador. Guayas:* Guayaquil (D. L. Frizzell); Milagro (H. E., D. L. Frizzell).

Argyrodes jamaicensis new species

Figures 261-265; Map 8

Type. Male from Rio Cobre Gorge, St. Catherine Parish, Jamaica, British West Indies, Nov. 6, 1957 (A. M. Chickering), in the Museum of Comparative Zoology. The specific name is an adjective.

Description. Male. Carapace, mouthparts, sternum dull yellowish brown; palpi brighter. Legs brownish yellow ringed with reddish brown. Abdomen brown, red, and silvery white, speckled; a pair of very small silver spots above spinnerets. Carapace with cephalic part narrow and coming to a blunt anterior point. Anterior median eyes a little larger than others, separated by nearly a diameter, farther from anterior lateral eyes. Seen from above, anterior row recurved; posterior row nearly straight with eyes equidistant. Clypeus rather low, straight above groove, bulging forward abruptly below groove, and narrowed to blunt point (Fig. 261). Abdomen with a pair of pointed lateral humps behind spinnerets, rounded behind humps, extending little behind spinnerets. Total length 2.4 mm. Carapace 1.3 mm long. First femur, 1.8 mm; patella and tibia, 2.2 mm; metatarsus, 1.1 mm; tarsus, 0.6 mm.

Female. Carapace, sternum dull brown. Mouthparts, clypeus yellow. Legs yellow ringed with reddish brown. Abdomen gray thickly covered with silvery white spots and dark brown streaks. The pair of silvery white spots above spinnerets larger than in male. Abdomen (Fig. 263) similar but shorter, wider and higher than that of male. Total length 2.3 mm. Carapace 0.9 mm long. First femur, 1.6 mm; patella and tibia, 1.6 mm; metatarsus, 0.7 mm; tarsus, 0.6 mm.

Variation. Some specimens are darker, others paler than those described. A couple of male specimens are very dark with only a few white spots. The humps of the abdomen vary in size and are much reduced in several males. In one female the lateral humps are widespread, long and pointed. All males are approximately the same size. Females vary in total length from 1.7 to 2.3 mm.

Diagnosis. Argyrodes jamaicensis is similar to *A. americanus, A. globosus* and *A. cubensis.* The shape of the male clypeus (Fig. 261), and the higher radix of the palpal bulb, with its shallower anterior margin and more nearly straight tip (Fig. 262) separate it from the others. The conductor of the bulb is similar to that of *A. caudatus* but lacks the projection. The embolus is slender, forming a very small coil, visible through the transparent radix. The tegulum is sclerotized and slightly rugose. The epigynum has a large oval depression in front of the scape. The lateral margins that extend from the scape spiral around the fossae, which contain the openings (Fig. 265). The large spherical seminal receptacles are almost touching. Tubes are simpler than in the other two species, without loops (Fig. 264). The abdomen is often similar to that of *A. globosus*, but the color differs. The wider scape of the epigynum (Fig. 265) separates *A. jamaicensis* from *A. globosus* and *A. cubensis.*

Distribution. Only known from Jamaica; Map 8.

Records. Jamaica. (MNHN). St. Thomas Par.: Holland Bay (A. M. Nadler); Lyssons (A. M. Nadler); 10 km NE of Bath; Bawden (both A. M. Chickering). Hanover Par.: Dolphin Head Trail (A. M. Chickering). St. Catherine Par.: Rio Cobre Gorge; Guanaboa Vale (both A. M. Chickering). St. Andrew Par.: Hardwar Gap, Blue Mts. (A. M. Chickering; A. F. Archer).

Argyrodes cubensis new species

Figures 266-270; Map 8

Type. Male from La Bayamesa, 1900 m elev., Oriente, Cuba "7/3/1955" (A. F. Archer), in the American Museum of Natural History. The species name is an adjective.

Description. Male. Carapace brownish, dusky around margin; clypeus reddish. Sternum dark brown. Legs brown. Abdomen with a silvery stripe on each side, a black mark behind each lateral hump. Dorsum dusky. Venter brown anterior to spinnerets, black behind with a pair of white marks, side by side, immediately behind spinnerets. Carapace slightly raised in eye region with a deep groove below anterior median eyes and clypeus projecting and hanging below chelicerae (Fig. 266). Anterior median eyes slightly larger than others, their diameter apart. Posterior median eyes two and one-half diameters apart. Abdomen extended behind spinnerets. Total length 3.0 mm. Carapace 1.8 mm long. First femur, 2.2 mm.

Female. Carapace darker than in male, brown. First femora brown, other leg segments whitish with darker bands. Abdomen silvery except for black venter and posterior; two silvery spots behind spinnerets. Carapace with groove below eyes and clypeus slightly bulging. Eyes closer together than in male. Abdomen shorter than that of male (Fig. 268). Total length 2.2 mm. Carapace 0.9 mm long. First femur, 1.2 mm; patella and tibia, 1.3 mm; metatarsus, 0.7 mm; tarsus, 0.4 mm.

Diagnosis. The elongate abdomen separates this species from *A. jamaicensis* and *A. globosus.* The palpus is similar but the tegulum is shorter (Fig. 267). The scape of the epigynum is much narrower than that of *A. jamaicensis,* and resembles that of *A. globosus.*

Record. Cuba. ♀ paratype collected with type.

Argyrodes maculosus O.P.-Cambridge

Figures 271-275; Map 9

Argyrodes maculosa O.P.-Cambridge, 1898, Biologia Centrali-Americana, Araneidea, vol. 1, p. 258, pl. 37, fig. 3. Female syntypes from Teapa, [Tabasco], Mexico, in the Hope Department of Entomology, Oxford University, examined by Levi.

Description. Male from Mexico. Carapace, sternum yellowish brown with clypeus yellow. Legs and mouthparts yellow with some gray. Posterior two pairs of legs annulate. Abdomen pale gray on dorsum with metallic silvery spots, especially on sides of dorsum; venter and lower part of sides reddish gray, a pair of silvery spots above spinnerets. Carapace slender; cephalic part narrowed between lateral and anterior median eyes, clypeus unusually high (Fig. 271). Anterior median eyes slightly larger than others and about a diameter apart, forming a square with

posterior median eyes; anterior laterals and posterior medians in a straight line and about equidistant. Abdomen short with a median and lateral pair of low humps and another pair of very low humps on posterior face, midway between spinnerets and dorsum. Total length 2.6 mm. Carapace 1.3 mm long. First femur, 2.4 mm; patella and tibia, 2.6 mm; metatarsus, 1.5 mm; tarsus, 0.9 mm. Another specimen had total length 2.2 mm.

Female. Carapace paler than that of male. Abdomen grayish white, streaked with dark gray and many small silvery spots. Genital area dark brown, a pair of bright silvery spots above spinnerets. Clypeus high and straight, with anterior median eyes projecting and a deep groove under eyes. Abdomen similar to that of male with three posterior humps (Fig. 273). Posterior pair of humps above spinnerets not easy to see. Total length 2.1 mm. Carapace 0.9 mm long. First femur, 1.4 mm; patella and tibia, 1.6 mm; metatarsus, 1.0 mm; tarsus, 0.6 mm. A second female, barely mature, measured 1.6 mm long.

Variation. A male collected in Florida shows some slight differences in position of the ducts and embolus. The carapace is like that of other specimens.

Diagnosis. Argyrodes maculosus is similar to *A. subdolus, A. spinosus,* and *A. tacter.* The very high clypeus of the male (Fig. 271) separates it from the first two, and the inconspicuous embolus (Fig. 272) from *A. tacter.* The female is separated from other species by the relatively small genital plate (Fig. 275) with its short scape, and by the internal genitalia with a wide tube from each opening forming a semicircle, then sharply bending anteriorly and becoming very slender before entering seminal receptacles. The receptacles are well separated (Fig. 274). The posterior hump on the abdomen of *A. maculosus* does not develop the two pair of points found in some other species, but is of variable length, much longer in the syntypes than in more recently collected specimens.

Distribution. Florida, eastern and southern Mexico; Map 9.

Records. United States. Florida. Highlands Co.: Highland Hammock, Sebring, April 2, 1957, ♂ (W. J. Gertsch, R. Forster). *Mexico. San Luis Potosí:* Tamazunchale, July 6, 1941 (L. I. Davis); May 20, 1952 (W. Cazier, W. J. Gertsch, R. Schrammel); 8 km N of Tamazunchale, July 2, 1941 (A. M., L. I. Davis). *Veracruz:* La Buena Ventura, July 1909 (A. Petrunkevitch).

Argyrodes taeter new species

Figures 276-280; Map 9

Type. Male from Xilitla, San Luis Potosí, Mexico, Dec. 2, 1939 (A. M. and L. I. Davis), in the American Museum of Natural History. The specific name is a Latin adjective meaning horrid.

Description. Male. Carapace yellowish brown, sternum a little darker. Legs yellowish, with dark rings. Abdomen mostly light gray, darker gray posteriorly, thickly covered with metallic golden to silvery spots. Carapace with extremely high clypeus (Fig. 276). Anterior median eyes less than a diameter apart. Abdomen extending a little behind spinnerets with a pair of posterior, lateral and median humps which are indistinct. Total length 2.2 mm. Carapace 1.3 mm long. First femur, 2.0 mm; patella and tibia, 2.0 mm; metatarsus, 1.2 mm; tarsus, 0.8 mm.

Female. Carapace dull brown with legs a little paler and the posterior three pairs with dark rings. Abdomen darker than in male with dark brown paired streaks above, and spotted with silvery flecks. Posterior surface mostly brown with a pair of inconspicuous silvery spots above spinnerets. Genital area orange-brown. Carapace rather wide, clypeus high, slightly bulging beneath shallow groove under eyes. Eyes as in male, but closer together. Abdomen high with small lateral humps, and posteriorly a small median dorsal hump (Fig. 278). Total length 1.9 mm. Carapace 0.6 mm long. First femur 1.4 mm; patella and tibia, 1.4 mm; metatarsus, 0.6 mm; tarsus, 0.5 mm.

Diagnosis. The carapace (Fig. 276) is similar to that of *A. maculosus*, the eye region is shorter, the groove deeper and wider. The palpus (Fig. 277) is a little heavier than in *A. maculosus;* the embolus forming a large conspicuous spiral, visible through transparent radix. The radix and conductor are similar to those of *A. caudatus*. Epigynum with a blunt scape. Some sections of connecting canals show between scape and lateral walls of fossae (Fig. 280). The ducts are wider and longer than those of *A. maculosus* (Fig. 279).

Records. Mexico. San Luis Potosí: Xilitla, ♀ ♂ paratypes collected with type; Nov. 30, 1940, ♀ paratype (A. M., L. I. Davis).

Argyrodes ululans O.P.-Cambridge

Figures 281-285; Map 9

Argyrodes ululans O.P.-Cambridge, 1880, Proc. Zool. Soc. London, p. 336, pl. 30, fig. 14. Male, female syntypes from the Amazon, [Brazil], in

the Hope Department of Entomology, Oxford University, examined by Levi.

Argyrodes socius Chamberlin and Ivie, 1936, Bull. Univ. Utah, biol. ser., vol. 3, no. 5, p. 40, pl. 10, figs. 90, 91. Female type from Barro Colorado Island, Panama, at the University of Utah, genitalia missing, examined by Exline. NEW SYNONYMY.

Description. Male from Panama Canal Zone. Carapace, mouthparts, legs brown with tarsi and basal part of metatarsi lighter; sternum darker. Abdomen nearly black with a longitudinal pale stripe that includes a few bright silvery spots on each side, a pair of silvery spots above spinnerets. There is considerable color variation. Carapace broad at eye region with clypeus swollen, deeply grooved (Fig. 281). Eyes approximately equal in size, with two rows close together; anterior eyes equidistant, a little over a diameter apart; posterior eyes forming straight line, with medians one and one-half diameters apart, nearer lateral eyes. Chelicerae slender with three teeth on anterior margin of fang groove, one tooth and a row of long fine denticles on the posterior margin. Abdomen greatly extended behind spinnerets with posterior tip turned down. Total length 4.0 mm. Carapace 1.5 mm long. First femur, 3.3 mm; patella and tibia, 3.5 mm; metatarsus, 2.4 mm; tarsus, 0.7 mm. Males vary from 3.3 to 4.5 mm long (one specimen only 2.8 mm long), length depending on extent of abdomen.

Female from Panama Canal Zone. Color as in male but more variable. Older females may become pale but some are reddish or nearly black with dark brown legs. Carapace with nearly parallel sides, blunt behind, narrowing in cephalic region. Clypeus moderately high. Abdomen as in male though heavier and not so long (Fig. 283). In gravid specimens the abdomen becomes very heavy and elongate. Total length 3.7 mm. Carapace 1.4 mm. long. First femur, 2.6 mm; patella and tibia, 2.7 mm; metatarsus, 1.6 mm; tarsus, 0.8 mm.

Variation. Length of females varies from 3.0 to 5.0 mm, depending mostly on age and development of ovaries. A female specimen from Fonte Boa, Amazonas, Brazil, was 6.5 mm long, with carapace 1.5 mm long. Its epigynum had an additional short transverse anterior lip overhanging a slight depression. This structure was best seen in slightly posterior view. The ends of this structure were slightly anterior to the anterior margin of lateral fossae.

Diagnosis. Argyrodes ululans is larger than other *Argyrodes* species from Panama and easily distinguished. It differs from

A. leonensis by having a seam on swollen portion of the male clypeus (Fig. 281), the coil of the embolus small, and the radix high with bluntly recurved tip (Fig. 282). The ducts in the median apophysis and tegulum are unlike those of other species. The female has a conspicuous wide scape with a fossa on each side (Fig. 285). The internal genitalia are illustrated by Figure 284.

Natural History. Dr. Chickering found some specimens in the webs of *Nephila clavipes* (Linnaeus).

Distribution. Southern Mexico to northern Brazil; Map 9.

Records. Mexico. Chiapas: Tapachula, Aug. 1909 (A. Petrunkevitch). *Panama.* El Valle, July 1936. *Panama Canal Zone.* Gamboa, July 1954 (A. M. Chickering); Barro Colorado Isl. (numerous coll.). *Venezuela. Aragua:* Maracay, 1935, 1936 (P. C. Vogl, ZSM). *Carabobo:* San Estebán, 1888 (E. Simon, MNHN). *Brazil.* (O.P.-Cambridge, 1880). *Amazonas:* Fonte Boa (de Mathan, MNHN).

Argyrodes bryantae new species

Figures 286-288; Map 9

Argyrodes maculosus, Banks, 1909, Proc. Philadelphia Acad. Sci., vol. 61, p. 205. Not *A. maculosus* O.P.-Cambridge.

Type. Male from Boquete, Panama, Aug. 1-8, 1950 (A. M. Chickering), in the Museum of Comparative Zoology. This species is named in memory of Miss Elizabeth B. Bryant, arachnologist, friend, and benefactress.

Description. Carapace yellowish brown, orange on clypeus. Sternum, mouthparts brown. Anterior legs mostly yellowish brown, posterior legs yellow with brown streaks and rings. Abdomen pale gray thickly covered with bright silvery spots, and dark gray patches on dorsum, and posterior side. Carapace gently inclined from thoracic groove to anterior margin, which is broadly rounded. Clypeus high with seam dividing it into equal halves, extending a little over base of chelicerae (Fig. 286). Eyes equal in size, posterior eyes about two diameters apart. Abdomen extended beyond spinnerets, with a pair of lateral humps a little behind spinnerets and a posterior extension, bifid at tip. Total length 3.2 mm. Carapace 1.4 mm long. First femur, 3.1 mm; patella and tibia, 3.5 mm; metatarsus, 2.4 mm; tarsus, 1.1 mm.

Female. Carapace and sternum dark, as in male. Legs reddish brown, with distal segments yellow and posterior legs annulate yellow and reddish brown. Abdomen darker than in male with a

pattern of three pairs of large black patches and a couple of median markings on dorsum with posterior side black; sides and venter as in male. Carapace low. Clypeus rather low with groove under eyes, somewhat bulging anteriorly. Anterior median eyes larger than others, over one diameter apart. Other eyes closer together than in male. Abdomen smaller, flattened dorsally, less extended behind, but with comparable protuberances (Fig. 288). Total length 2.5 mm. Carapace 1.0 mm long. First femur, 1.7 mm; patella and tibia, 1.8 mm; metatarsus, 1.0 mm; tarsus, 0.6 mm.

Variation. A male from northern Panama has the dorsal part of the clypeus higher, receding to seam, with chelicerae weaker and placed below lateral eyes so that clypeus protrudes farther.

Diagnosis. The male clypeus of *A. bryantae* (Fig. 286) is similar to that of *A. dracus*. The posterior extension of abdomen is sometimes conspicuously bifid (Fig. 288). The palpus is large, rounded. The radix is high with anterior margin almost straight, ending in a hook. Unlike related species, *A. bryantae* has the median apophysis unusually thick ventrally, crossed by three uneven, diagonal parts of the tube (Fig. 287). Embolus narrow, forming small spiral mostly covered by radix. The conductor resembles that of *A. caudatus*. Epigynum has a long scape, as in *A. dracus* but not so bulging posteriorly. Seminal receptacles small; tubes very narrow and spiralled posteriorly, enlarging greatly to arch anterior to receptacles, then narrowing abruptly before entering them. (Epigynum of the only female specimen is lost.)

Records. Costa Rica. Santa María Dota, ♂ (Tristan). *Panama.* Boquete, 2 ♂ paratypes collected with type; El Volcán, Chiriquí, Feb. 1936, ♂ (W. J. Gertsch).

Argyrodes spinosus Keyserling

Figures 289-291; Map 9

Argyrodes spinosus Keyserling, 1884, Die Spinnen Amerikas, Theridiidae, pt. 1, p. 201, pl. 9, fig. 121. Male lectotype here designated from Amable María, [Dept. Junín], Peru, in the Polish Academy of Sciences, Warsaw, examined by Levi. (Not Keyserling, 1891, *op. cit.*, Brasilianische Spinnen, p. 214, pl. 8, fig. 155.)

The illustrations were prepared from the lectotype.

The only specimen which might be this species is a male from Hacienda Corosal, near La Silla Mt., Dist. Fed., Venezuela, 1888 (E. Simon, MNHN), which has a longer embolus, and a shorter duct loop in the tegulum, but has a similar clypeal bulge.

This species differs from *A. dracus* by the shorter embolus and bulging clypeus.

Argyrodes gapensis new species

Figures 292-294; Map 9

Type. Female from Hardwar Gap, Jamaica, Nov. 17, 1959 (A. M. Nadler), in the American Museum of Natural History. The specific name is a latinized adjective derived from a geographical name.

Description. Female. Carapace and sternum gray infused with red. Legs red banded with pale yellow. Abdomen background very pale, mottled with red and silver and with horizontal streaks of dark gray on sides and posterior. Clypeus nearly straight with groove under eyes obscure. Anterior median eyes a little larger than others, over a diameter apart, and forming a square with posterior median eyes. Lateral eyes near median eyes. Abdomen extended above rather than behind spinnerets, with a pair of conspicuous humps above spinnerets and a median dorsal protuberance (Fig. 292). Protuberance with four obscure points and with cuticle deeply wrinkled. Total length 2.6 mm. Carapace 1.2 mm long. First femur, 1.9 mm; patella and tibia, 2.0 mm; metatarsus, 1.0 mm; tarsus, 0.5 mm.

Diagnosis. Color and shape of abdomen unlike that of other West Indian species. Epigynum similar to that of *A. caudatus*, with scape a little longer and excavation anterior to it deeper (Fig. 294). A pair of conspicuous, large, round median bulges between fossa and genital groove. Seminal receptacles and anterior part of tubes (Fig. 293) as in *A. cancellatus*, with posterior part of tubes not twisted as in *A. caudatus* and *A. cancellatus*.

Argyrodes sicki new species

Figures 295-299; Map 9

Type. Male from Sumaré, 200-300 m elev., Cidade Rio de Janeiro, Brazil, Jan. 1946 (H. Sick), in the American Museum of Natural History. The species is named for Dr. H. Sick.

Description. Male. Carapace and sternum dark brown with clypeus and legs lighter brown, posterior three pairs of legs annulate brown and yellow. Abdomen dark gray with a few lines and small spots of silver. Carapace broad and quite blunt in front. Clypeus straight and only slightly sloping forward under anterior median eyes to a deep cleft. Cleft with nearly circular

lateral excavations covered by setae, and medially closed by lips. Below cleft, clypeus bulges anterior to and overhanging base of chelicerae (Fig. 295). Anterior median eyes larger than others, and closer together than posterior median eyes. Posterior eyes in nearly straight line if viewed from above, posterior medians separated by two and one-half diameters, by less than two from laterals. Abdomen extending a little above and behind spinnerets with a pair of pointed lateral humps, and ending above in an upper and two lower pointed tips. Total length 2.7 mm. Carapace 1.3 mm long. First femur, 2.9 mm; patella and tibia, 2.3 mm; metatarsus, 1.3 mm; tarsus, 0.8 mm.

Female. Color as in male but abdomen lighter gray; dorsum more or less outlined with rows of silvery spots and a diamond-shaped mark in middle of dorsum, two lines of silvery spots on sides, and a group of silvery spots anterior to tip. Clypeus high with anterior median eyes projecting over it. Abdomen a little higher and wider than in male, but with similar pointed protuberances (Fig. 297). Total length 2.5 mm. Carapace 0.8 mm long. First femur, 1.4 mm; patella and tibia, 1.5 mm; metatarsus, 0.8 mm; tarsus, 0.6 mm.

Variation. Size and shape are not very variable, but the humps on the abdomen are very small and not pointed in some specimens. Carapace and legs of some specimens are darker than in others.

Diagnosis. The shape of the abdomen is similar to that of *A. caudatus* and *A. dracus.* The high male clypeus with the cleft near the ventral margin (Fig. 295) separates *A. sicki* from *A. dracus.* The palpus of the male is similar to that of *A. dracus,* but more slender. The radix is long, with the anterior margin concave, ending medially in a long recurved bluntly pointed arm. The fleshy basal portion of the embolus is conspicuous; the sclerotized coiled end is mostly under the transparent radix. The conductor has a ventral, rectangular, membranous arm, and a long, sharp sclerotized tooth lying against the cymbium on the mesal side (Fig. 296).

The epigynum of the female is vaulted anteriorly, sloping to a median scape. The lateral margins of the scape curve around the fossae (Fig. 299). A pair of large round openings with sclerotized edges lie in the fossae and open to an inner sclerotized chamber (Fig. 298), perhaps similar to *A. argyrodes* group. The seminal receptacles are small, anterior to the anterior wall. The tubes are difficult to see. They lie in the mesal wall of the vaulted sclerotized chamber, and empty directly into the receptacles

(Fig. 298). No other species known has spherical chambers such as found in *A. sicki*.

Natural History. The species has been collected from webs of *Nephila*.

Distribution. Southeastern Brazil; Map 9.

Records. Brazil. Rio de Janeiro: Sumaré, Cidade Rio de Janeiro, 200-400 m elev., Jan.-March 1946, ♀ ♂ paratypes (H. Sick); Teresópolis, 900-1000 m elev., March 1946 (H. Sick).

Argyrodes caudatus (Taczanowski)

Figures 300-322; Map 10

Ero caudatus Taczanowski, 1872 (1873), Horae Soc. Ent. Rossicae, vol. 10, p. 63. Male, female syntypes from Uassa, French Guiana [Uaçá, Amapa, Brazil], in the Polish Academy of Sciences, examined by Levi.

Argyrodes sextuberculata O.P.-Cambridge, 1880, Proc. Zool. Soc. London, p. 335, pl. 30, fig. 13. Male, female syntypes from Amazon, Brazil, in the Hope Department of Entomology, Oxford University, examined by Levi. NEW SYNONYMY.

Argyrodes felix O.P.-Cambridge, 1880, *ibid.*, p. 340, pl. 30, fig. 19. Female type from Paraná, Brazil, in the Hope Department of Entomology, Oxford University, examined by Levi. NEW SYNONYMY.

Argyrodes caudatus, Keyserling, 1884, Die Spinnen Amerikas, Theridiidae, pt. 1, p. 198, pl. 9, fig. 119. Petrunkevitch, 1930, Trans. Connecticut Acad. Sci., vol. 30, p. 182, figs. 23-26.

Argyrodes cylindrica Franganillo, 1936, Los Aráchnidos de Cuba, Havana, p. 57, figs. 22, 23. Types from Oriente, Cuba, probably lost. NEW SYNONYMY.

Argyrodes parvior Chamberlin and Ivie, 1936, Bull. Univ. Utah, biol. ser., vol. 3, no. 5, p. 37, figs. 85, 86. In part, female only. (Male type = *A. americanus*.)

Argyrodes vexus Chamberlin and Ivie, 1936, *ibid.*, p. 39, figs. 76-78. Male type from Panama Canal Zone, in the American Museum of Natural History, examined by Exline. NEW SYNONYMY.

Conopistha caudata, Bryant, 1940, Bull. Mus. Comp. Zool., vol. 86, no. 7, p. 306.

Conopistha obtusa, Bryant, 1940, *ibid.*, p. 308. Caporiacco, 1948, Proc. Zool. Soc. London, vol. 118, p. 649, fig. 56. Not *A. obtusus* O.P.-Cambridge.

Conopistha manta Exline, 1945, Ann. Ent. Soc. America, vol. 38, p. 524, figs. 24-33. Holotype from Manta, Manabí, Ecuador, in the California Academy of Sciences. NEW SYNONYMY.

Description. Male from Panama Canal Zone (compared with type). Carapace, mouthparts, sternum, and femora, patellae and tibiae of first two pairs of legs light brown. Other legs and segments pale yellow with brown and red annulations. Dorsum and posterior side of abdomen tan, outlined with dark gray streaks

and with some irregular gray markings and dull silvery spots. Sides mostly covered with silver. Venter silver, red and black, with genital and lung areas brown. Carapace lowest at thoracic groove, wide at lateral eyes, then abruptly narrowed in front to width of anterior median eyes. Anterior median eyes largest, projecting slightly over clypeus, about a diameter apart, as far from posterior medians and farther from anterior laterals. Median eyes forming a square. Posterior eyes in recurved row, about equidistant, widely separated. Lateral eyes sometimes separated. Clypeus rather low. Groove near eyes closed, narrow; below groove, clypeus nearly straight, very slightly projecting in middle. Chelicerae long (Figs. 300-306). Abdomen extended far beyond spinnerets, with a pair of posterior lateral humps, and a blunt median posterior hump with a trace of four points. Total length 4.3 mm. Carapace 1.8 mm long. First femur, 3.3 mm; patella and tibia, 3.9 mm; metatarsus, 2.4 mm; tarsus, 0.9 mm.

Female from same collection. Carapace, sternum and legs colored as in male. Dorsum and posterior side of abdomen light brown with a few dull silver spots and outlined with groups of spots. Sides and venter speckled brown and silver. Epigynum and lung cuticle light brown. Carapace smoother than that of male. Eyes much closer together. Anterior median eyes largest and about a diameter apart. Clypeus moderately high, slightly rounded beneath a shallow groove under eyes. Abdomen extending beyond spinnerets with a pair of low lateral humps, and a median posterior hump with two dorsal points and two more widely spaced ventral points (Fig. 319). Total length 3.5 mm. Carapace 1.3 mm long. First femur, 2.1 mm; patella and tibia, 2.4 mm; metatarsus, 1.3 mm; tarsus, 0.6 mm.

Figures 307, 314, 320 were prepared from the syntypes of *Ero caudatus*.

Variation. Size, color and shape of abdomen are extremely variable. Males vary in length from 2.5 to 5.3 mm; females from 2.2 to 4.0 mm. Color varies from very pale to dark, and some specimens have a reddish cast. The pattern of the abdomen is conspicuous in some specimens; a few specimens have dorsum black with sides a bright contrasting silver; in others the dorsum is dark gray bordered with narrow streaks of black and a broad band of bright silver. Many specimens (especially from Panama) are almost black with only a few silvery spots. Pale specimens have the abdomen light gray or tan, sometimes streaked with darker gray and partially covered with dull silvery spots; a few

specimens have the abdomen almost all dull silver. The shape of the abdomen varies from broadly oval with low lateral and posterior humps, to elongate, extended considerably beyond the spinnerets, and with or without conspicuous humps. The posterior projection may end in conspicuous fleshy points, or these may be almost non-existent.

Size and distance between eyes are variable, but the shape of the carapace and clypeus is fairly constant (Figs. 300-306). The clypeal shape is most variable in Texas and Mexico (Figs. 303-306); that of a specimen from southern Brazil also differs (Fig. 300). The lateral eyes may be separated. The tip of the male radix varies in length; the tip of the conductor is long, sometimes rather conspicuous, and sometimes almost invisible. The width of the fossae of the epigynum is variable, and the anterior margin may be almost straight or may have a small, rounded, median lip (Figs. 320-322). One female from Tingo María, Peru, has a noticeably sclerotized scape. One specimen from Cuba has the scape unusually long, but the internal genitalia as in other specimens. The position of the anterior loops of the duct is extremely variable in different individuals and also geographically. They loop anterior to the seminal receptacles (as in *A. cancellatus*) in Mexican specimens (Fig. 318); in specimens from Panama one side may be anterior but not the other. The duct is narrowed near seminal receptacles in most specimens except those from Mexico (Figs. 311-316). The duct is most variable in southern and eastern Brazil (Figs. 311-313) and some specimens may belong to a different species (Fig. 311). Specimens from Mexico in general resemble *A. cancellatus*.

Some intermediates are found in southern Florida, Bimini, Cuba and Dominican Republic. Females have the epigynum less swollen, as in *A. caudatus*, but the internal genitalia are as in *A. cancellatus*. One female from Jamaica and one from San Estebán, Venezuela, thought to be *A. caudatus*, had internal genitalia similar to those of *A. cancellatus*. Several males have the carapace high as in *A. cancellatus*, the clypeus straight as in *A. caudatus*, and the palpus much wider than that of *A. caudatus*. Males of *A. caudatus* have been collected with females having these intermediate characters in Monroe County, Florida and Bimini. Males were collected with other *A. caudatus* males in Bimini and Cuba. Two males from the Dominican Republic mountains have the clypeus intermediate; one male has the palpus (Fig. 310) somewhat like that of *A. cancellatus*, the other has a

shorter tegulum loop but a longer embolus [Loma Lucilla Mts., Cordillera Central, 1500-2000 m elev., June 1938 (P. J. Darlington); between Constanza and Lomo Cibao, Aug. 1958 (A. F. Archer)].

A much larger number of specimens is needed to study this variation in detail, and in particular, to understand the specimens believed to be intermediate with *A. cancellatus*.

Diagnosis. Males of *A. caudatus* can be separated from those of *A. cancellatus* by the straight rather than bulging clypeus and by the longer chelicerae. The anterior median eyes are usually larger than the others (Figs. 300-306). The females have the epigynum (Figs. 320-322) flat behind the openings, not swollen as in *A. cancellatus*. The internal ducts are shorter and not fused (Figs. 311-318).

Distribution. Southern Texas, Florida to southern Brazil; Map 10.

Records. United States. Florida. Dade Co.: Miami, 1903, ♂ (J. Comstock). Monroe Co.: Tavernier, ♀ ♂, Nov. 29, 1952 (A. M. Nadler); Palmetto Key (C. M. Breder). *Texas.* Hidalgo Co.: Edinburg, 1933, ♂ (S. Mulaik); 7 mi. E of Edinburg, Oct. 14, 1936, ♂ (S. Mulaik); S of Pharr, Apr. 5, 1936, ♂ (S. Mulaik). *Mexico. Tamaulipas:* near El Limón (C. M. Goodnight); 10 km E of Villa Juárez (L. I. Davis). *San Luis Potosí:* 8 km N of Tamazunchale (A. M., L. I. Davis); Valles (L. Steude). *Veracruz:* Cordoba (J. C., D. L. Pallister); 24 km E of Pánuco (A. M., L. I. Davis); Tecolutla (M. Johnston, A. M. Davis). *Chiapas:* Tonala (A. Petrunkevitch). *Costa Rica.* Río Anonos (Tristan); San José (E. Schmidt). *Panama.* La Campana (E. Fiehter). *Panama Canal Zone.* Forest Reserve; Ancon; Cocoli; Experimental Gardens; Miraflores Lock; Summit; Ft. Sherman; Chilibre; France Field; Madden Dam; Chiva Rd.; near Pedro Miguel; Farfan; Ft. Randolph; Summit Park; Arraiján; El Valle; Fort Davis; Balboa; Barro Colorado Isl.

Bahama Isl. South Bimini (A. M. Nadler); Grand Bahama Isl. (Hayden, Rabb). *Cuba.* Oriente: Banes (A. F. Archer). Villas: Soledad (P. J. Darlington; L. G. Worley). Matanzas: Pan de Palenque (A. F. Archer). Pinar del Rio: Sierra de Anafe (M. Barro). *Jamaica.* Trelawny Par.: Rd. to Adelphi. St. Andrew Par.: Kingston. St. Catherine Par.: Guanaboa Valley; near Bushby; near Spanish Town. St. Thomas Par.: Morant Bay Rd. Clarendon Par. Portland Par.: Hardwar Gap. *Dominican Republic.* Colonia Ramfis, Trujillo Váldez (A. F. Archer); Puerto

Plata (D. Hurst); near La Romana (Hassler). *Puerto Rico.* E of San Sebastián Collazo (A. F. Archer); Mayagüez (A. F. Archer; A. M. Nadler); N of Las María Mts. de Urayan (A. F. Archer); Rio Piedras (A. M. Nadler); Cuevas de los Alfanos, Barro Mona (A. F. Archer); ?Rubianes (A. F. Archer); Arecibo (A. M. Nadler). *Virgin Isl.* St. Thomas Isl. (A. F. Archer). St. John (A. F. Archer). St. Croix: Christianstad (A. M. Nadler; H. A. Beatty). *Lesser Antilles. St. Vincent Isl.* (MNHN). *Trinidad:* (MNHN); Gasparee (R. H. Montgomery); Mt. St. Benedict (J. G. Myers). *Aruba.* (A. M. Nadler).

Venezuela. Aragua: Maracay (A. M. Nadler). *Dist. Fed.:* La Guaira, Caracas (E. Simon, MNHN). *Carabobo:* San Estebán (E. Simon, MNHN). *British Guiana.* Sauri-wau River, near Tacutu (W. G. Hassler). *French Guiana.* Cayenne (A. M. Nadler). *Ecuador.* Guayas: 5 km N of Manglar Alto (E. I. Schlinger, E. S. Ross); 13 km S of Manglar Alto (E. I. Schlinger, E. S. Ross). *Peru. Loreto:* Pebas (M. de Mathan, MNHN). *Huánuco:* Monzon Valley, Tingo María (E. I. Schlinger, E. S. Ross). *Brazil. Pará:* Santarém (MNHN). *Ceara:* Serra Communaty (MNHN). *Bahía:* Condeúba (E. Gounelle, MNHN); Salvador (MNHN). *Espírito Santo:* Santa Teresa (A. M. Nadler). *São Paulo:* Jequirituba, São Paulo (H. Sick). *Paraguay. Alto Paraná:* Taquararapá.

Argyrodes cancellatus (Hentz)

Figures 323-336; Map 10

Theridion cancellatum Hentz, 1850, Proc. Boston Soc. Nat. Hist., vol. 6, p. 278, pl. 9, figs. 17, 18. Types from Alabama, lost. 1875, The spiders of the United States, p. 149, pl. 16, figs. 17, 18.

Lasaeola cancellata, Emerton, 1882, Trans. Connecticut Acad. Sci., vol. 6, p. 26, pl. 5, fig. 4.

Argyrodes larvatus Keyserling, 1884, Die Spinnen Amerikas, Theridiidae, pt. 1, p. 197, pl. 9, fig. 118. Male type from Columbus, [Colorado Co.], Texas, in the United States National Museum.

Bellinda cancellata, Keyserling, 1884, *op. cit.,* pt. 1, p. 216, pl. 10, fig. 130.

Argyrodes cancellatus, Keyserling, 1886, *op. cit.,* pt. 2, p. 243, pl. 20, fig. 297. Emerton, 1909, Trans. Connecticut Acad. Sci., vol. 14, p. 184, pl. 1, fig. 10. Bonnet, 1955, Bibliographia Araneorum, vol. 2, pt. 1, p. 709.

Conopistha cancellata, Kaston, 1948, Bull. Connecticut Geol. Nat. Hist. Surv., no. 70, p. 88, pl. 4, figs. 80-84.

Conopistha partita, Chamberlin and Ivie, 1944, Bull. Univ. Utah, biol. ser., vol. 8, no. 5, p. 38. Archer, 1946, Paper Alabama Mus. Nat. Hist., no. 22, p. 28.

Note. Although this species had been widely known for nearly a hundred years as *Argyrodes cancellatus* (Hentz), Chamberlin and Ivie (1944) suggested that the name is a synonym of *Theridion partitum* Walckenaer (1841, Histoire naturelle des Insectes Aptères, vol. 2, p. 323). However, Abbot's drawing in the British Museum, to which Walckenaer gave the name, is not diagnostic.

Description. Male from Lawrence County, Alabama. Carapace brown. Legs light brown near body, with distal part of femora and other segments darker; posterior legs paler with joints dark brown. Abdomen dark gray speckled with white or dull silver spots. Carapace flat, gradually and only slightly raised to eye region. Head broad, bluntly rounded in front. Eyes small, anterior medians very little larger than others, separated by about a diameter, farther from lateral eyes. Posterior eyes equidistant, nearly three diameters apart. Lateral eyes slightly but distinctly separated. Clypeus high, receding beneath anterior median eyes to groove, then bulging to a blunt point in front of and below base of chelicerae (Figs. 323-331). Groove hidden by setae from above and below. Chelicerae heavy, short, about equal to height of clypeus. Abdomen elongate, extending behind spinnerets with a pair of lateral humps and a median posterior projection with two pairs of points. Total length 3.8 mm. Carapace 1.7 mm long. First femur, 3.0 mm; patella and tibia, 3.5 mm; metatarsus, 2.3 mm; tarsus, 1.1 mm.

Female from same collection. Color and pattern as in male. Carapace as in male but shorter. Clypeus high with wide shallow groove under eyes, bulging below groove. Eyes as in male except medians nearer to laterals. Abdomen shorter, not extending so far behind spinnerets, rounder, higher, with similar humps (Fig. 335). Total length 3.2 mm. Carapace 1.2 mm long. First femur, 1.9 mm; patella and tibia, 2.2 mm; metatarsus, 1.3 mm; tarsus, 0.7 mm.

Variation. Size and color are variable in all populations. Males measure from 2.5 to 4.5 mm; females from 2.3 to 3.5 mm. Individuals from New York, North and South Carolina, and Arkansas are larger than those from Florida, Mississippi and Louisiana. Pale and dark specimens are found in most populations. The carapace and legs are mostly yellow or pale gray; abdomen pale gray and silver, or sometimes nearly all silvery in pale specimens. In dark specimens, the carapace may be almost black, or deep brown, and abdomen dark gray to black with only a few gray and silver spots. Some specimens, especially from the Northeast,

have a golden cast, with the carapace reddish brown and the abdomen speckled with red, gray and silver. The posterior median eyes vary from two to three diameters apart; lateral eyes may be nearly contiguous to over a radius apart. The male clypeus usually recedes in the middle at the groove, then bulges and protrudes below the base of the chelicerae, but the extent of the protrusion is variable (Figs. 323-331). The scape of the epigynum in some specimens projects ventrally; in some it is more rounded. In some specimens the humps of the abdomen are poorly developed; in a few they are exaggerated. The dorsal pair of posterior points are united in many specimens.

Diagnosis. Argyrodes cancellatus is similar to *A. caudatus,* but is separated by having the anterior edge of the male clypeus bulging, the chelicerae much shorter (Figs. 323-331), and the anterior margin of head rounded. The male palpus is similar, but usually more rounded in outline. Females usually have the abdomen shorter and rounder (Fig. 335) than that of *A. caudatus.* The epigynum is larger and bulges behind scape (Fig. 337). The seminal receptacles are very small, round, and close together. The tubes are longer, and loop anterior to receptacles; unlike those of *A. caudatus,* they are fused together into sclerotized masses posteriorly (Figs. 333-334). The separation of some female specimens is difficult and the genitalia may have to be cleared. It has been collected with *A. caudatus* in southern Florida and Bahama Islands, and some specimens seem to be intermediate. A female from Jamaica and one from San Estebán, Venezuela, first thought to be *A. caudatus,* have sclerotized internal genitalia like *A. cancellatus.*

Natural History. Argyrodes cancellatus has been collected in New York in webs of *Epeira strix* [*Araneus cornutus* (Clerck)]; and under stones by J. H. Emerton; in webs of *Agelenopsis* by W. J. Gertsch; in *Agelenopsis* webs in Mississippi by H. Exline; and in webs of *Nephila clavipes* (Linnaeus) in Louisiana by H. Exline. Archer (1946) reports it in Alabama in webs of "*Allepeira lemniscata, Argiope aurantia, Metepeira labyrinthea, Nephila clavipes,* and *Verrucosa arenata.* It is also found in the webs of *Frontinella pyramitela,* and in cave entrances in the webs of *Theridion tepidariorum* and a species of *Pholcus.*" Several individuals may live in one host web. The egg-case is small and round with a wide posterior lip, and hangs by strong threads. Several egg-cases are often found together.

Distribution. Eastern North America; Map 10.

Records. Canada. Ontario. East Sister Isl., Lake Erie (J. A. Beatty). *United States. New Hampshire.* Hillsborough Co.: Hollis. *Connecticut.* Fairfield Co.: Norwalk (R. V. Chamberlin). New Haven Co.: New Haven (J. H. Emerton). *New York.* Suffolk Co.: Cold Spring Harbor (sev. coll.). *Pennsylvania.* Berks Co.: Shillington (L. Hook). *Ohio.* Hocking Co.: Rockbridge. Ottawa Co.: South Bass Isl. (J. A. Beatty). *District of Columbia.* (Fox). *Virginia.* Brunswick Co.: Alberta. Fairfax Co.: Falls Church (N. Banks); Mt. Vernon. *Kentucky.* Breathitt Co.: Noble (L. Giovannoli). Edmonson Co.: Mammoth Cave. *Tennessee.* Bedford Co.: Shelbyville (A. F. Archer). Davidson Co.: Nashville (A. R. Laskey). Grundy Co.: Bersheeba. *North Carolina.* Carteret Co.: Lennox Pt. (R. D. Barnes). Durham Co.: Durham (J. H. Emerton); Duke Forest (H., L. Levi; R. D. Barnes). Orange Co.: Chapel Hill (J. H. Emerton). *South Carolina.* Charleston (J. H. Emerton). *Florida.* Collier Co.: Royal Palm Hammock (S. Rounds). De Soto Co.: W of Arcadia (W. J. Gertsch). Hillsborough Co.: Hillsborough Riv. State Park (W. J. Gertsch). Gadsden Co.: Quiney (W. J. Gertsch). Gulf Co.: Wewahitchka. Lake Co.: Leesburg (M. Statham). Liberty Co.: Torreya State Park (W. J. Gertsch). Monroe Co.: Tavernier (A. M. Nadler). Pinellas Co.: Dunedin (W. S. Blatchley). Seminole Co.: Longwood (W. J. Gertsch). *Alabama.* Baldwin Co.: Lagoon (A. F. Archer). De Kalb Co.: De Soto State Park (A. F. Archer). Mobile Co.: Mobile (A. F. Archer); Dauphin Isl. (A. F. Archer). Tuscaloosa Co.: Tuscaloosa (A. F. Archer). Winston Co.: Bankhead Natl. Forest (A. F. Archer). *Mississippi.* Clarke Co.: Shubota (H. E. Frizzell). Jackson Co.: Pascagoula (H. E. Frizzell). Warren Co.: Vicksburg (H. E. Frizzell). Wilkinson Co.: Centreville (A. F. Archer). *Louisiana.* Ascension Par.: Donaldsonville (H. E. Frizzell). *Missouri.* Phelps Co.: 10 mi. S of Rolla (H. E. Frizzell). *Arkansas.* Washington Co.: Cove Creek Valley (M. Hite). *Texas.* Denton Co.: Clear Creek (S. Jones). Liberty Co.: Liberty (S. Mulaik). Robertson Co.: Easterly (H., D. Frizzell). San Augustine Co.: San Augustine (S. Mulaik). Tyler Co.: Woodville (L. I. Davis). Walker Co.: Huntsville (S. Mulaik).

Bahama Isl. South Bimini, ♀ (W. J. Gertsch, M. A. Cazier).

Argyrodes darlingtoni new species

Figures 337-341; Map 11

Type. Female from rain forest near Valle Nuevo, 2000 m elev., Dominican Republic, Aug. 1938 (P. J. Darlington), in the Museum of Comparative Zoology. The species is named in honor of the collector.

Description. Male. Carapace, sternum, legs dusky yellow. Legs annulate, especially posterior legs. Sternum with median longitudinal gray stripe. Abdomen pale gray with dorsum outlined in darker gray, with dark streaks, especially behind humps and at tip, sparsely covered with dull silvery spots. Cephalic region narrowed. Clypeus rather high, nearly straight with a seam (Fig. 337). Eyes approximately equal in size. Anterior median eyes over a diameter apart, nearer lateral eyes than in related species. Posterior median eyes a diameter and a half apart and nearer lateral eyes. Abdomen elongate, dorsum flattened with a pair of low lateral humps and a posterior projection with three fleshy, pointed tips. Total length 3.3 mm. Carapace 1.2 mm long. First femur, 2.0 mm; patella and tibia, 2.3 mm; metatarsus, 1.4 mm.

Female. Carapace yellow-brown, becoming yellow on clypeus and chelicerae. Legs annulate yellow and brown. Sternum yellow, brown posteriorly. Abdomen pale gray, streaked and somewhat mottled with dark gray and dull silver. Clypeus rounded, nearly straight. Anterior median eyes a little larger than others, otherwise similar to eyes of male. Abdomen shorter, wider, higher than in male, somewhat flattened on dorsum, with a low pair of lateral humps, a pair of conspicuous humps above spinnerets, and a short posterior tubercle, ending in three short blunt tips (Fig. 339). Total length 2.7 mm. Carapace 1.1 mm long. First femur, 1.7 mm; patella and tibia, 1.8 mm; metatarsus, 0.8 mm; tarsus, 0.6 mm.

Diagnosis. Male palpus similar to that of *A. caudatus* with radix shorter, ending in a hook that is widened and truncate at its end (Fig. 338). Embolic spiral a little wider than in *A. caudatus.* Female epigynum with a broad scape, wide and blunt. Openings closer together than in related species, and tubes leading from them visible far to the sides (Fig. 341). Unlike *A. quasiobtusus, A. darlingtoni* has the ducts enter the seminal receptacles on the anterior lateral side (Fig. 341) and the duct lumina inside the fused sclerotized bodies are distinct. The sexes have been matched on the basis of similar color pattern and abdominal humps.

Distribution. Jamaica, Haiti; Map 11.

Records. Jamaica. 1 km E of Reading, St. James Par., June 23, 1954, ♀. *Haiti.* 2 km E of Cayes du Jacmel, Sept. 2, 1935, ♂ (W. G. Hassler); 40 km from Aux Cayes, 700-1000 m elev., Aug. 29, 1935, ♂ (W. G. Hassler).

Argyrodes godmani new species

Figures 342-346; Map 11

Argyrodes maculosus, F.P.-Cambridge, 1902, Biologia Centrali-Americana, Araneidea, vol. 2, p. 405 (in part), pl. 38, figs. 12, 13, 13a (not fig. 13b = *A. convolutus*). Not *A. maculosus* O.P.-Cambridge.

Type. Male from Guatemala, 1896-1901 (F. Sargent), in the Godman collection in the British Museum (Natural History). The specific name is in honor of the former owner of the collection.

Description. Male. Carapace, sternum and legs yellow; posterior legs annulate. (Abdomen missing.) Carapace low, rounded in front. Clypeus high with deep groove, closed in center, with wide excavations at sides, and protruding ventrally as a blunt point over base of chelicerae (Fig. 342). Anterior median eyes very large, only their radius apart. Posterior eyes not so widely spaced as in related species; medians nearer laterals than each other. Carapace 1.2 mm long. First femur, 1.7 mm; patella and tibia, 2.2 mm; metatarsus, 1.4 mm.

Female. Carapace and legs colored as in male. Abdomen tan with large splashes and streaks of tiny silvery spots. Carapace as in male with anterior median eyes large but farther apart. Clypeus moderately high, straight. Abdomen high, rounded, with small lateral humps above spinnerets and a very small posterior tubercle with a tiny median dorsal spine, and a pair of tiny ventral spines (Fig. 344). Total length 2.7 mm. Carapace 1.2 mm long. First femur, 1.8 mm; patella and tibia, 2.1 mm; metatarsus, 1.0 mm; tarsus, 0.6 mm.

Diagnosis. The male resembles *A. dracus,* but the clypeus is higher, has a deeper more dorsal groove, and the eyes are larger (Fig. 342). The palpus has a long radix, ending in a hook; the embolus forms a large spiral (Fig. 343). The epigynum has a long, rather slender scape, with sides extending in wide sclerotized arches, leaving a narrow fossa with conspicuous openings (Fig. 346). The seminal receptacles are small. A wide heavily sclerotized tube forms a half spiral, from the end of which arises a narrow tube connecting it with the receptacles (Fig. 345). The shorter duct separates this species from *A. dracus.*

Record. Guatemala. 2 ♀ paratypes collected with type.

Argyrodes quasiobtusus new species

Figures 347-351; Map 11

Type. Male from St. John, Virgin Islands, July 10-12, 1958 (A. F. Archer), in the American Museum of Natural History. The specific name is a compound Latin adjective, meaning almost blunt.

Description. Male. Carapace dusky, yellow on head and clypeus. Legs pale yellow with dusky and reddish brown annulations. Sternum mottled reddish brown and yellow. Abdomen with entire dorsum dark gray to black. Sides, posterior and venter grayish white with dull silvery spots. Carapace flat, narrowed and rounded in front. Clypeus moderately high, straight, with median seam, and slightly overhanging base of chelicerae (Fig. 347). Eyes about equal in size, all farther apart than in related species; anterior median eyes very distant from laterals. Abdomen narrow, sides undulating; a pair of humps above spinnerets; projecting bluntly behind, bifurcate at posterior tip. Total length 3.6 mm. Carapace 1.5 mm long. First femur, 2.3 mm; patella and tibia, 2.6 mm; metatarsus, 1.5 mm.

Female. Carapace dark gray infused with yellow, yellow on clypeus and mouthparts. Legs pale yellow, ringed with reddish brown. Sternum yellow with reddish markings. Abdomen dorsum dark gray to black, paler gray in center. Sides and venter whitish, mottled with dark gray, reddish brown, and dull silver. Carapace flat. Clypeus moderately high, somewhat rounded under groove. Eyes larger than those of male and closer to each other. The shape of the abdomen as in male (Fig. 349). Total length 2.5 mm. Carapace 1.0 mm long. First femur, 1.6 mm; patella and tibia, 1.7 mm; metatarsus, 0.8 mm.

Diagnosis. The shape of the abdomen and eyes of male are distinctive. The male palpus is similar to that of *A. caudatus*, with shorter radix, ending in widely recurved slender tip. The dorsal arm of the conductor is tooth-like, projecting ventrally (Fig. 348). The scape of the epigynum is long and bluntly pointed with openings large and lateral (Fig. 351). The scape is flat, without a bulge behind it, separating it from *A. dracus*. The seminal receptacles are of moderate size; the coils of tubes are fused and sclerotized in a pair of bodies (Fig. 350) a little shorter than those of *A. darlingtoni*. The sexes have been matched on the basis of the similarity of pattern and shape of abdomen.

Distribution. Puerto Rico, Virgin Islands; Map 11.

Records. Puerto Rico. El Yunque, Sierra Luquillo, Aug. 7, 1957, ♀ (A. F. Archer); Las Cruces, March 28, 1930, ♀ (Leonard); Maricao Forest, June 2-3, 1938, ♂ (P. J. Darlington).

Argyrodes dracus Chamberlin and Ivie

Figures 352-358; Map 11

Argyrodes maculosus, F.P.-Cambridge, 1902, Biologia Centrali-Americana, Araneidea, vol. 2, p. 405, pl. 38, figs. 12, 12a, 13b, *not* figs. 13, 13a. Not *A. maculosus* O.P.-Cambridge.

Argyrodes dracus Chamberlin and Ivie, 1936, Bull. Univ. Utah, biol. ser., vol. 3, no. 5, p. 38, figs. 73-75, *not* figs. 88, 89, ♀. Male holotype from Barro Colorado Island, Panama Canal Zone, lost.

Conopistha spinosa, Exline, 1945, Ann. Ent. Soc. America, vol. 38, p. 522, figs. 34-37. Not *A. spinosus* Keyserling.

Comments. This species has erroneously been called *A. maculosus* in North American collections. In collections from South America, *A. dracus* has been confused with *A. convolutus* and *A. spinosus.*

Description. Male from Panama Canal Zone. Carapace, sternum, mouthparts orange-yellow, infused with gray. Legs similar but posterior legs with reddish brown annulations. Abdomen gray sometimes with a reddish cast, and many silvery white spots. Cephalic part of carapace rounded in front. Clypeus straight, high, and extending ventrally over base of chelicerae, with short shallow groove below eyes (Figs. 352, 353). Anterior median eyes a little larger than others, separated by about a diameter, farther from anterior laterals; median ocular area almost square, a little wider behind; posterior eyes equally spaced. Abdomen short, extending little behind spinnerets with a pair of lateral pointed humps, and two postero-dorsal pairs of pointed tips sometimes borne on a single protuberance. All tips inconspicuous in some specimens. Total length 2.6 mm. Carapace 1.3 mm long. First femur, 2.2 mm; patella and tibia, 2.5 mm; metatarsus, 1.3 mm; tarsus, 0.8 mm.

Female. Coloration as in male. Carapace broad, clypeus moderately high, almost vertical with a narrow groove below anterior eyes, and slightly bulging below groove. Abdomen (Fig. 355) similar to that of male, but usually wider and higher; protuberances not so conspicuous and sometimes barely evident. Not much variability in shape of abdomen between young and gravid females. Total length 2.3 mm. Carapace 0.8 mm long. First femur, 1.5 mm; patella and tibia, 1.6 mm; metatarsus, 0.7 mm; tarsus, 0.6 mm.

Variation. Males vary in length from 2.4 to 3.0 mm; females from 1.6 to 2.5 mm. The hook of the male radix, usually rounded, is sometimes straightened toward the tip, and there is some variation in size. In some specimens the scape of the female epigynum is rebordered. The distal part of the connecting canals is enlarged and then abruptly narrowed before entering the receptacles in some Panamanian specimens and in females from Paraguay. In older females the posterior convolutions of the connecting canals are surrounded by cuticle, the canals are grown together, and may be heavily sclerotized (Fig. 356). The abdominal protuberances are evident in some specimens, not in others. A male from San Luis Potosí has the carapace bright yellow, the legs lacking annulations, and the abdomen pale gray with silvery spots. A male from Chiapas also is pale, but has annulate legs. A male from Paraguay is paler than most specimens from Panama, and has the posterior legs slightly annulate, the hook of the radix somewhat straightened, and the tip and the embolus not so heavily sclerotized.

Diagnosis. Argyrodes dracus is very similar to *A. godmani, A. chickeringi* and *A. subdolus* in size and general appearance, although the latter two lack the abdominal pointed tips of *A. dracus.* Males are separated from most related species in having the clypeus straight and slightly produced over the base of chelicerae (Figs. 352, 353). The width of the male palpus and small hook at tip of its radix (Fig. 354) separate it from *A. chickeringi.* It is separated from *A. maculosus* by the characters of the clypeus, and from *A. godmani* by shape of clypeus, somewhat wider embolic tube and narrower hook on radix. Females are separated from the other species by the tapering, pointed scape, directed ventrally, and by the bulge posterior to it (Figs. 357, 358).

Distribution. Southern United States to Paraguay; Map 11.

Records. United States. Alabama. Houston Co.: Dothan, 1939, ♀ (A. F. Archer). *Mexico. San Luis Potosí:* Tamazunchale, (L. I. Davis). *Oaxaca:* Tolosa (B. Malkin). *Chiapas:* Las Ruinas de Palenque (C., M. Goodnight). *Panama Canal Zone.* Barro Colorado Isl. (many coll.); Fort Randolph; Fort Davis; Experimental Gardens; France Field; Boquete; Madden Dam; Summit; Pedro Miguel; Forest Reserve (all A. M. Chickering). *Venezuela.* [probably northern Venezuela coll. by Simon] (MNHN). *Ecuador. Guayas:* Milagro (Exline, 1945). *Brazil.* Espírito Santo (Keyserling, 1891, in part). *Paraguay. Alto-Paraná:* Teguarapa [? = Tacuara], ♀ ♂.

Argyrodes chickeringi new species

Figures 359-364; Map 11

Type. Male from Barro Colorado Island, Panama Canal Zone, July 30, 1936 (A. M. Chickering), in the Museum of Comparative Zoology. This species is named for Dr. Chickering.

Description. Male with carapace, chelicerae and legs bright yellowish brown; sternum darker. Abdomen dull black or gray with a pair of contiguous whitish spots on posterior part of dorsum and a broad whitish band separating dorsum from sides, the white parts having a few silvery flecks. A pair of round silvery spots above spinnerets. Venter brownish gray. Clypeus moderately high, greatly receding at groove and slightly overlapping base of chelicerae (Fig. 360). Groove two-thirds height of clypeus from ventral edge, and thickly bordered with setae. Eyes small. Anterior median eyes largest and separated by a diameter, farther from posterior median and lateral eyes. Posterior eyes forming a very recurved line, equally and widely spaced. Abdomen extended only a little behind and above spinnerets, without humps but somewhat angular at posterior lateral extremity and faintly protuberant at posterior extremity. Total length 3.3 mm. Carapace 1.5 mm long. First femur, 2.4 mm; patella and tibia, 2.6 mm; metatarsus, 1.6 mm; tarsus, 1.0 mm. The three males are very similar.

Female. Color and pattern as in male but slightly darker and without the dorsal pair of light spots. Carapace flatter than in male. Clypeus moderately high with a very narrow groove under eyes, rounded and nearly vertical. Anterior median eyes farther apart, but nearer lateral eyes. Abdomen almost like that of male but very blunt behind, partially wrinkled (Fig. 362). Total length 3.2 mm. Carapace 1.4 mm long. First femur, 2.6 mm (other segments missing).

Diagnosis. Male similar to *A. dracus* with clypeus swollen below groove (Fig. 360). The palpus (Fig. 361) very similar to that of *A. dracus* but slightly narrower and hook of radix not bent. The embolus wide, forming a wide, exposed spiral (Fig. 361). Epigynum (Fig. 364) as in *A. maculosus* and *A. dracus*, but it differs from that of *A. dracus* in having the posterior area less swollen, and from that of *A. maculosus* by the longer scape and the internal genitalia. Seminal receptacles small, separated by a diameter; tubes of large diameter forming two tight coils posteriorly, and then narrowing and forming one large loop to enter heavily sclerotized receptacles (Fig. 363). The lack of

banding of third and fourth legs and smooth posterior tip of the abdomen (Fig. 362) also separate this species from *A. dracus*.

Record. Panama Canal Zone. Barro Colorado Isl., 1 ♀, 2 ♂ paratypes collected with type.

Argyrodes subdolus O.P.-Cambridge

Figures 365-369; Map 11

Argyrodes linguata O.P.-Cambridge, 1898, Biologia Centrali-Americana, Araneidea, vol. 1, p. 259, pl. 38, fig. 1. Male holotype from Santa Ana, Guatemala, in the British Museum (Natural History), examined by Levi.

Argyrodes subdola O.P.-Cambridge, 1898, *op. cit.*, p. 260, pl. 38, fig. 2. Female holotype from San Antonio, near the city of Guatemala, [Guatemala], in the British Museum (Natural History), examined by Levi. F.P.-Cambridge, 1902, Biologia Centrali-Americana, Araneidea, vol. 2, p. 405, pl. 38, fig. 11.

Argyrodes obtusus, F.P.-Cambridge, 1902, *op. cit.*, vol. 2, p. 403, pl. 38, fig. 3. Not *A. obtusus* O.P.-Cambridge.

Notes. Specimens in collections have been misidentified as *A. trituberculatus, A. obtusus,* and *A. maculosus.* The name *subdolus* is selected rather than *linguatus.* Though *linguatus* has page priority, it has never been used.

Description. Male from Texas. Carapace dusky yellow. Sternum shiny, dusky. Mouthparts, clypeus and palpi dark orange. Abdomen gray, irregularly spotted with silver. Carapace narrow anteriorly and arched in front (Fig. 365). Clypeus high, not overlapping chelicerae, with a short shallow groove. Posterior tip of abdomen extending above, but not much posterior to spinnerets, a small pair of humps present. Total length 2.8 mm. Carapace 1.4 mm long. First femur, 2.5 mm; patella and tibia, 2.8 mm; metatarsus, 1.7 mm; tarsus, 0.9 mm.

Female. Carapace and legs dusky yellow to brown, sternum darker. Abdomen dark gray with irregular streaks and patches of white or silver. Carapace broader than in male. Clypeus moderately high, straight somewhat bulging below groove. Abdomen heavier than that of male, with more conspicuous lateral humps. Posterior tip usually blunt but sometimes extending behind as a three-pointed projection (Fig. 367). Total length 2.6 mm. Carapace 1.2 mm long. First femur, 1.7 mm; patella and tibia, 1.8 mm; metatarsus, 1.2 mm; tarsus, 0.7 mm. Females vary from 2.2 to 2.6 mm.

Diagnosis. Males of *A. subdolus* can readily be separated from others of the *A. cancellatus* group by two teeth on the radix, visible in ventral view (Fig. 366). The embolus forms a large coil and the conductor has a small ventral projection. The long narrow scape of the epigynum (Fig. 369) is diagnostic. The coils of the connecting canals (Fig. 368) are sclerotized and fused as single structures.

Distribution. Texas, Arizona, Mexico, south to Guatemala; Map 11.

. *Records. United States. Texas.* Bell Co.: Temple (L. I. Davis). Hidalgo Co.: Edinburg (S. Mulaik); Hidalgo (L. I. Davis). Leon Co.: Jewett (L. I. Davis). Sutton Co.: 28 mi. E of Sonora (W. J. Gertsch). Travis Co.: near Austin (H. E. Frizzell). *Arizona.* Santa Cruz Co.: Madera Canyon (W. J. Gertsch, L. Hook). *Mexico. Nuevo León:* 24 km S of Monterrey (W. J. Gertsch); Linares (L. I. Davis); Horsetail Falls (W. J. Gertsch). *Hidalgo:* Jacala (L. I. Davis). *Veracruz:* Tecolutla (H. M. Wagner). *Jalisco:* Ajijic (A. F. Archer). *Colima:* Miramar, Manzanillo (F. Bonet). *Michoacan:* Conjumatlan (L. I. Davis). *Distrito Federal:* Tenango (H. Wagner). *Guerrero:* Mexcala (L. I. Davis). *Chiapas:* San Cristóbal de las Casas (C., M. Goodnight); Cintalapa (H. Wagner); Las Cruces (H. Wagner). *Guatemala.* Chichicastenango (C., P. Vaurie).

Argyrodes davisi new species

Figures 370-374; Map 12

Type. Male from Big Tree Vine Association, Cameron County, Texas, Sept. 1936 (L. I. Davis), in the American Museum of Natural History. The species is named after the collector.

Description. Male. Carapace grayish brown, yellow anteriorly with a pair of brown longitudinal lines behind eyes and a pair of transverse markings connected to lines. Anterior legs yellowish proximally, becoming dark brown toward ends of femora, other segments dark. Posterior legs yellow with faint reddish brown annulations. Sternum yellow, brown posteriorly and in median line. Abdomen light gray, mostly covered with silvery spots. Carapace short, evenly raised to posterior eye region, where it is wider than in most species, terminating bluntly in front of posterior eyes. Clypeus high with groove under anterior median eyes; groove thickly covered with short, dorsally curved setae; clypeus bulging in front of and below base of chelicerae (Fig. 370). Anterior median eyes on anterior face of head; only

slightly larger than other eyes; separated by less than a diameter, farther from laterals and posterior medians. Eyes of posterior row slightly recurved; posterior medians separated by nearly three diameters, not so far from laterals. Abdomen short and wide, with prominent lateral humps above spinnerets, and a median blunt posterior hump ventral to laterals. Total length 2.8 mm. Carapace 1.4 mm long. First femur, 2.2 mm; patella and tibia, 2.5 mm; metatarsus, 1.5 mm; tarsus, 0.7 mm.

Female. Carapace and sternum uniform grayish brown; anterior legs a little paler than in male, terminal segments annulate. Abdomen darker than in male, dorsum mostly without silver spots. Carapace similar to that of male without modified clypeus or widened cephalic region; anterior median eyes on anterior surface as in male. Clypeus high with wide shallow groove under eyes. Anterior median eyes farther apart than in male, no larger than posterior medians; other eyes all nearer each other than in male. Abdomen wider and higher than in male with humps exaggerated and lateral humps pointed (Fig. 372). Total length 2.3 mm. Carapace 0.8 mm long. First femur, 1.4 mm; patella and tibia, 1.4; metatarsus, 0.7 mm; tarsus, 0.5 mm.

Variation. The female from Chiapas has the tube of the genitalia unevenly coiled, and the coils are at an acute angle to the genital groove rather than in the longitudinal axis.

Diagnosis. Argyrodes davisi is smaller than, but related to, *A. leonensis* and *A. ululans.* The shape of the male clypeus (Fig. 370) separates them. The cymbium of the male palpus is short. The radix is long but unusually narrow, concave on anterior margin, ending in a blunt recurved tip. The embolus forms a very narrow spiral under radix (Fig. 371). The epigynum is small with a moderately long pointed scape (Fig. 374). Outline of fossae visible only on anterior margin. Seminal receptacles very large, more widely separated than in *A. leonensis,* with narrow tubes forming several tight, even, horizontal spirals before entering receptacles (Fig. 373).

Distribution. Texas to Chiapas; Map 12.

Records. United States. Texas. Cameron Co.: 1 ♀ paratype, 1 juv. collected with holotype. *Mexico. Chiapas:* Finca Santa Marta, near Huehuetán, July 31, 1950, ♀ (C., M. Goodnight).

Argyrodes amates new species

Figures 375-379; Map 12

Type. Female from Los Amates, Guatemala, 1908 (Kellerman), in the Museum of Comparative Zoology. The specific name is a noun in apposition after the type locality.

Description. Male. Carapace, sternum, legs brownish yellow. Abdomen gray, darker posteriorly, covered with rather large, bright silvery plates. Carapace very low, rounded in front, broad at lateral eyes. Clypeus low with deep, open groove under eyes, bulging under groove anterior to eyes and chelicerae (Fig. 375). Anterior median eyes a little larger than others. Posterior eyes widely and equally spaced. Abdomen extended beyond spinnerets, widened above just behind spinnerets, but with no real humps, then narrowed to form a blunt posterior tip. Total length 3.2 mm. Carapace 1.5 mm long. First femur, 2.7 mm; patella and tibia, 3.2 mm; metatarsus, 2.0 mm.

Female. Carapace and legs similar to those of male but more yellowish. Abdomen yellow with smaller silvery spots, a large gray basal area on dorsum, and only ventral half of posterior side dark gray, with a pair of silver spots above spinnerets. Carapace not as low as in male. Clypeus low, nearly straight. Abdomen high with a pair of low lateral humps and a very blunt posterior tubercle (Fig. 377). Total length 2.3 mm. Carapace 0.9 mm long. First legs missing.

Diagnosis. The bulge of the male clypeus (Fig. 375) distinguishes *A. amates* from related species. The palpus has a short radix with straight tip. The conductor as in *A. caudatus,* but with dorsal arm extended ventrally as a large fleshy tooth (Fig. 376). The epigynum of female with short, pointed scape (Fig. 379). The seminal receptacles are large. The ducts distinguish this species from *A. caudatus* and other related species. There are three spirals, the one closest to the seminal receptacles being the largest. The proximal portion of duct is wavy and is enclosed by the spiralled portion (Fig. 378).

It is not certain that the male and female belong together. Both have a dark patch on the abdomen posterior to the spinnerets, enclosing two light spots, side by side.

Distribution. Chiapas, Guatemala; Map 12.

Records. Mexico. Chiapas: Tenejapa, July 22, 1950, ♂ (C. Goodnight).

Argyrodes peruensis new species

Figures 380-384; Map 12

Type. Male from Santa Teresa on the Río Huallaga, 600 m elev., Huánuco, Peru, Aug. 1954 (F. Woytkowski), in the American Museum of Natural History. The specific name is an adjectival form of Peru.

Description. Male. Carapace dusky yellow with gray infusions and a median longitudinal black line. Femora pale near body, becoming dusky orange distally; distal leg segments dusky orange. Sternum black anteriorly, yellow posteriorly. Abdomen yellowish white with some irregular dark gray lines, all dark gray behind and at sides of spinnerets, and gray at posterior dorsal tip. Large silvery spots are scattered on dorsum, a pair above spinnerets, and several under tip. Carapace unusually low and wide. Clypeus very high, nearly straight, with wide shallow groove in middle (Fig. 380). Anterior median eyes larger than others, separated by less than a diameter, nearer posterior median eyes, which are separated by nearly two diameters. Abdomen rounded, ending in small bluntly pointed, almost ventral, tubercle. Total length 2.2 mm (abdomen damaged). Carapace 1.1 mm long. First femur, 2.0 mm; patella and tibia, 2.2 mm; metatarsus, 2.0 mm; tarsus, 1.0 mm.

Female. Carapace dusky yellow, gray on margin, in midline, and along cephalic grooves. Legs as in male except not so pale near body. Sternum black and yellow. Abdomen similar to male, but with dorsum dark gray at base; and silver on posterior under tubercle. Carapace similar to that of male. Clypeus moderately high with wide groove under eyes, nearly straight with anterior median eyes projecting over clypeus. Eyes similar to those of male but anterior medians a little farther apart. Abdomen nearly spherical with small posterior tubercle about midway between spinnerets and highest point of abdomen (Fig. 382). Total length 2.2 mm. Carapace 0.8 mm long. First femur, 1.3 mm; patella and tibia, 1.3 mm; metatarsus, 0.9 mm; tarsus, 0.6 mm.

Variation. A second male is 2.5 mm in total length and is darker.

Diagnosis. The spherical abdomen with small posterior tubercle, and dark gray-silver coloration distinguish *A. peruensis* from related species. The radix of the male palpus is wide, reaching almost to ectal side of cymbium, and has a small hook on anterior face (Fig. 381). The embolus forms a much wider spiral than

that of *A. caudatus*. The epigynum is small with a moderately wide, short fossa, bordered anteriorly with heavily sclerotized rims that fuse in center as a blunt, somewhat protruding scape (Fig. 384). The openings are small, at lateral ends of the fossae. The tubes spiral twice tightly to midline, then the spiral reverses, with two more loops. There are several large loops on the side of the seminal receptacles, before tubes enter them (Fig. 383). The receptacles are large, heavily sclerotized, spherical, separated by less than a diameter.

Records. Peru. Huánuco: Río Huallaga, ♀ ♂ paratypes collected with type.

Argyrodes subflavus new species

Figures 385, 386; Map 12

Type. Male from Divisoria, Huánuco, Peru, 1700 m elev., Oct. 1946 (F. Woytkowski), in the American Museum of Natural History. The specific name is a Latin adjective meaning yellowish.

Description. Male. Carapace golden yellow, infused with gray in posterior part. Clypeus, palpi, mouthparts and femora of legs golden yellow. Distal segments of legs infused with gray. Sternum gray. Abdomen cream with a gray patch on posterior part of dorsum and a narrow gray streak, bordered with silvery flecks, extending down each side to spinnerets. A narrow curved band of silvery flecks on each side in anterior third and a short band on each side of dorsum above spinnerets. Venter grayish with a central silvery spot. Carapace low, narrow, evenly and slightly inclined from posterior to anterior edge. Clypeus moderately high with very large, wide, open groove covered by setae (Fig. 385). Beneath groove, clypeus bulges, narrows and protrudes in front above chelicerae. Anterior median eyes much larger than others, and as in *A. argyrodes* well in front of other eyes, a little over a radius apart, well over a diameter from posterior median eyes. Posterior row of eyes strongly recurved. Median ocular area square. Abdomen rather slender, extending behind spinnerets. The posterior tip is rounded. Total length 3.0 mm. Carapace 1.4 mm long. Legs missing.

Diagnosis. The coloring, shape of clypeus (Fig. 385), size and position of eyes are diagnostic. The palpal structure is similar to that of *A. striatus,* but differs in that the radix reaches almost to the ectal side of palpus, and has a median anterior tooth (Fig. 386). The broad embolus lies in a wide spiral seen only through

the radix. The conductor is large, curved around the inner terminal part of the cymbium, and has a stout terminal tooth that protects the tip of the embolus. The female is unknown.

Records. Peru. Huánuco: Divisoria, ♂ paratype collected with type.

Argyrodes convolutus new species

Figures 387-389; Map 12

Argyrodes spinosus, Keyserling, 1891, Die Spinnen Amerikas, Brasilianische Spinnen, p. 214, in part; specimens from Espírito Santo, Brazil, collected by Göldi. Not *A. spinosus* Keyserling, 1884.

Type. Female from 69 km east of Tingo María, Dept. Huánuco, Peru, Oct. 5, 1954 (E. I. Schlinger, E. S. Ross), in the California Academy of Sciences. The specfic name is a Latin adjective, describing the loops in the female genitalia.

Description. Female. Carapace yellowish brown, legs paler and annulate. Abdomen gray, with darker gray patches and streaks and finely dotted with silvery flecks. Carapace wide, narrowed and rounded in front; clypeus almost straight, moderately high with anterior median eyes projecting over shallow groove. Abdomen high, not extending behind spinnerets, with a pair of blunt, postero-lateral humps, and a median postero-dorsal protuberance bearing two pairs of shiny points (Fig. 387). Total length 2.4 mm. Carapace 0.9 mm long. First femur, 1.5 mm; patella and tibia, 1.5 mm; metatarsus, 0.7 mm; tarsus, 0.6 mm.

Diagnosis. Female with large epigynum similar to that of *A. dracus,* but scape blunter, more posteriorly directed, rebordered, and tip spoon-shaped (Fig. 389). Posterior part only slightly projecting ventrally. The seminal receptacles are large, connecting canals of same diameter throughout and tightly spiralled with from five to eight loops (not always the same on the two sides of the same specimen) surrounding a series of smaller loops of the duct leading to the openings (Fig. 388). The presence of the scape separates females from those of *A. affinis,* and the internal genitalia from *A. dracus.* The male is not known. This species may be the female of *A. spinosus.*

Distribution. Central America to southeastern Brazil, apparently absent in Panama; Map 12.

Records. Guatemala. (F. D. Godman, BMNH). *British Guiana.* Upper Essequebo Riv., Onora Region, Dec. 20, 1937 (W. G. Hassler). *Peru. Huánuco:* Divisoria, 1700 m elev., Sept. 1946 (F. Woytkowski). *Brazil. Espírito Santo:* (E. Göldi, BMNH).

Argyrodes leonensis new species
Figures 390-394; Map 12

Type. Male from Horsetail Falls, Nuevo León, Mexico, June 11, 1936 (A. M., L. I. Davis), in the American Museum of Natural History. The species is named for the type locality.

Description. Male. Carapace, palpi and sternum chestnut brown, legs yellow. Abdomen dark gray with a longitudinal silver stripe on each side. Carapace low, wide in front. Eyes small, anterior medians slightly larger than others, posterior eyes separated by slightly more than two diameters, in a slightly recurved row if viewed from above. Clypeus high, slanting forward under anterior median eyes, forming a triangular lip (as viewed from above) over deep cleft. Clypeus bulging below cleft but scarcely overhanging chelicerae, partially divided by a median furrow (Fig. 390). Cleft somewhat obscured by setae. Abdomen elongate, extending far behind spinnerets, with low lateral humps midway between spinnerets and tip; tip blunt with wrinkled cuticle. Total length 4.6 mm. Carapace 1.7 mm long. First femur, 3.7 mm; patella and tibia, 4.1 mm; metatarsus, 2.6 mm.

Female with carapace and sternum chestnut brown, legs and abdomen reddish brown with a large silvery spot on each side posteriorly. Abdomen shorter and higher than that of male, sometimes rather pointed behind (Fig. 392). Total length 3.5 mm. Carapace 1.3 mm long. First femur, 1.8 mm; patella and tibia, 1.8 mm; metatarsus, 1.1 mm; tarsus, 0.7 mm.

Diagnosis. The shape of the male clypeus (Fig. 390) separates *A. leonensis* from *A. davisi* and *A. perucnsis.* The palpus with the long, narrow radix, ending in a short, blunt, recurved point (Fig. 391) separates the males from *A. ululans.* The embolus is slender, forming a very wide spiral. The conductor is large, more heavily sclerotized than in related species. The tegulum shows only a small portion of seminal duct (Fig. 391). The epigynum is fairly large, somewhat raised, dark, with broad, pointed, rebordered scape almost dividing the fossae (Fig. 394), and separating females from near relatives except *A. davisi.* The lateral openings are in deep fossae, leading into poorly sclerotized connecting canals tightly and evenly coiled around the straight sclerotized distal portion that leads to the seminal receptacles (Fig. 393).

Distribution. Mexico; Map 12.

Records. Mexico. Nuevo León: Horsetail Falls, June 11, 1936, ♂, 2♀ paratypes (A. M., L. I. Davis); Nov. 27, 1937, ♀ (L. I.

Davis, Brown). *Chiapas:* Tonalá, Aug. 1909, ♀ ♂ (A. Petrunkevitch).

Argyrodes alticeps Keyserling

Figures 395-399; Map 12

Argyrodes alticeps Keyserling, 1891, Die Spinnen Amerikas, Brasilianische Spinnen, p. 210, pl. 8, fig. 151. Male holotype from Espírito Santo, Brazil, in the British Museum (Natural History), examined by Levi. Simon, 1894, Histoire Naturelle des Araignées, p. 499.

Description. Male. Carapace, sternum, legs yellow. Abdomen grayish white with a few gray streaks and small silvery flecks. Cephalic region bearing anterior median and posterior median eyes, elongate, elevated and narrowed with parallel sides (Fig. 395). All median eyes anterior to lateral eyes. Median eyes forming a square. Abdomen extending a little behind and above spinnerets, widest just behind spinnerets with a pair of low lateral humps. Posterior tip of abdomen blunt. Total length 2.6 mm. Carapace 1.2 mm long. First femur, 2.3 mm; patella and tibia, 2.5 mm; metatarsus, 1.7 mm.

Female. Carapace orange-yellow with gray infusions, sternum a little darker. Legs pale yellow with first patella and tibia darker. Abdomen almost white with dark gray or tan on basal part of dorsum, a pair of oblique streaks near tip, lower sides and most of venter. Abdomen covered with fairly large silver spots. Clypeus as in other species, with a shallow groove under anterior median eyes. Median eyes forming a square as in male. Abdomen only moderately high and extended behind spinnerets with a pair of low lateral humps. Tip of abdomen bluntly tapered behind spinnerets (Fig. 397). Total length 2.3 mm. Carapace 1.0 mm long. First femur, 1.6 mm; patella and tibia, 1.6 mm; metatarsus, 1.0 mm; tarsus, 0.5 mm.

Figures 395, 396 were prepared from the type specimen.

Diagnosis. The projection of the eye region of the male (Fig. 395) is diagnostic. The radix is long with the tip recurved, bluntly pointed. The embolus forms a wide, heavy spiral (Fig. 396). The female has a large bulging epigynum with a blunt median anterior swelling. A long, slender sclerotized scape projects ventrally from the shallow fossa. The openings are lateral in fossae (Fig. 399). The seminal receptacles are large. Narrow tubes winding from the openings posterior to receptacles, then forming a lateral loop before entering the receptacles on the ventral side near their posterior lateral margin(Fig. 398). The

genitalia separate the species from *A. acuminatus*. Males and females were not collected together and it is not absolutely certain that they belong together.

Records. Paraguay. Alto-Paraná: Taguararapa, 2 ♂ ; Apa, 2 ♀ .

Argyrodes affinis O.P.-Cambridge

Figures 400-405 ; Map 12

Argyrodes affinis O.P.-Cambridge, 1880, Proc. Zool. Soc. London, p. 337, pl. 30, fig. 16. Male and female syntypes from Paraná, Brazil, in the Hope Department of Entomology, Oxford University, examined by Levi.

Description. Male from Santa Catarina, Brazil, (compared with type by Levi). Carapace, tarsi of palpi, sternum and mouthparts light brown, infused with gray. Legs and proximal segments of palpi yellow. Abdomen brown, almost covered on dorsum except over heart with silver, and silvery spots scattered elsewhere. Carapace short, cephalic part wide, bearing lateral eyes on low prominence. Clypeus high below shallow groove, bulging considerably beyond, but not over base of chelicerae. Thick covering of setae over groove (Fig. 400). Anterior median eyes a little larger than others, separated by nearly a diameter, farther from posterior medians and anterior laterals. Posterior median eyes separated by nearly three diameters. Abdomen highest and widest at spinnerets, greatly extended behind and a little above spinnerets, ending in blunt point (Fig. 402). Total length about 5.0 mm. Carapace 1.4 mm long. Anterior legs missing.

Female from São Paulo, Brazil. Carapace and sternum light brown infused with gray, carapace becoming yellow on anterior sides and clypeus. Legs yellow, grayish near joints; last two segments of palpi brown. Dorsum of abdomen yellow with silvery spots, a longitudinal dark gray line, and four brown and gray cross bars. Lower sides, venter, and posterior yellowish gray with scattered dull silvery flecks. Carapace narrow. Clypeus nearly straight, a little rounded ventral to deep groove under eyes, fairly high. Anterior median eyes a little smaller and more widely separated than in male and much closer to anterior lateral eyes. Abdomen extended behind spinnerets, widest behind spinnerets, with a pair of low lateral humps and a low posterior extension (Fig. 403) (abdomen damaged). Total length 2.2 mm. Carapace 0.9 mm long. Anterior legs missing.

Figures were prepared from the type specimens.

Variation. A second male from Santa Catarina has abdomen shorter. A third male, only 4.0 mm long, from same area, has a broad dark gray band on dorsum, and posterior side dark gray with a pair of silvery spots above spinnerets. The blunt tip shows indication of bifurcation.

Diagnosis. Argyrodes affinis is a large species. The male has a high, bulging clypeus and a broad eye region (Fig. 400). The palpus, similar to that of *A. striatus,* has the radix shorter and with a very concave anterior margin, ending in a much shorter, ventrally curved tooth (Fig. 401). The embolus is slender, forming a narrow spiral, visible only through radix. The conductor is lying entirely within the cymbium, large, terminating in a median, blunt, leaf-like part and an outer part with heavily sclerotized margin. The epigynum separates this species from others; it has a large, wide fossa with a transverse anterior margin, the median part of which projects as a ventral lip. A large lateral opening and three spirals are visible through the fossa wall on each side (Fig. 405). The seminal receptacles are rather small, joined to the openings by tubes forming four spirals on each side, without lateral or anterior loops (Fig. 404).

Distribution. Southern Brazil; Map 12.

Records. Brazil. São Paulo: São Paulo, 700-800 m elev., Dec. 1945, ♀ (H. Sick). *Paraná:* ♀ ♂ (O.P.-Cambridge, 1880). *Santa Catarina:* Nova Teutonia, lat 27°11′S, long 52°23′W, 3 ♂ (F. Plaumann, SMF).

Argyrodes rigidus new species

Figures 410-412; Map 12

Type. Female from Teresópolis, Est. Rio de Janeiro, Brazil, 900-1100 m elev., Nov. 7-9, 1945 (H. Sick), in the American Museum of Natural History. The specific name is a Latin adjective meaning "hard" or "stiff" referring to the cuticle of the female fossa.

Description. Carapace, mouthparts, and sternum pale reddish brown with some gray. Legs pale yellow, heavily banded with red and brown. Abdomen tan speckled with brown, red, and dull silvery spots, and with long black streaks on the sides and near tip; venter and posterior with a reddish cast. Another female is darker with abdomen mostly dull black streaked with reddish and silvery spots. Clypeus only moderately high, rounded to ventral edge under groove. Anterior median eyes largest, well separated; median eyes forming a square; lateral eyes almost

contiguous. Sternum very wide. Abdomen with low anterior dorsal humps, a pair of posterior lateral humps, and a low posterior median hump (Fig. 410). Total length 2.4 mm. Carapace 0.9 mm long. Anterior legs missing.

Diagnosis. Argyrodes rigidus is similar to *A. acuminatus* Keyserling, with the epigynum less swollen, and the fossa far wider (Fig. 412). The seminal receptacles are spherical, heavily sclerotized with tubes on each side forming five or six uneven posterior and lateral spirals between openings and receptacles (Fig. 411). However, their exact course is difficult to follow.

The male is unknown. This may be the female of *A. striatus*.

Records. Brazil. Rio de Janeiro: Teresópolis, 900-1100 m elev., March 1946, ♀ paratype (H. Sick).

Argyrodes striatus Keyserling

Figures 408, 409; Map 12

Argyrodes striatus Keyserling, 1891, Die Spinnen Amerikas, Brasilianische Spinnen, p. 213, pl. 8, fig. 154. Male type from Espírito Santo, Brazil, in the British Museum (Natural History), examined by Levi. Göldi, 1892, Mitt. Osterlande, neue Folge, vol. 5, pp. 224, 228.

Description. Male from Minas Gerais, Brazil. Carapace dusky yellow, clearer anteriorly. Legs pale yellow with light brown annulations. Sternum dusky yellow anteriorly, gray posteriorly. Abdomen grayish white with irregular dark gray markings and nearly covered on sides and dorsum with large silvery flecks. Posterior tip pale. Carpace low, wide, with cephalic part gradually elevated and wide. Eyes small, nearly equal, widely separated except contiguous lateral eyes. Anterior median eyes more than a diameter apart. Posterior median eyes nearly three diameters apart and nearly as far from anterior medians and posterior laterals. Clypeus rather low, straight beneath anterior median eyes to a shallow cleft, then jutting forward, rounded and narrowed in front of chelicerae (Fig. 408). Abdomen somewhat elongate with a pair of lateral tubercles on dorsum posterior to spinnerets, and a long median posterior tubercle ending in a pair of blunt tips. Total length 3.0 mm. Carapace 1.2 mm long. First femur, 1.7 mm; patella and tibia, 2.0 mm; metatarsus, 1.0 mm; tarsus, 0.6 mm.

Variation. A second male from Est. Santa Catarina, Brazil, is much darker, having carapace brown. The type has the cymbium of the palpus truncate (Fig. 409) and there is a slight possibility that two species are confused. The female is unknown; it may be *A. rigidus*.

Diagnosis. The shape of the clypeus (Fig. 408) is somewhat similar to *A. affinis*. The palpus is broad. The radix is wide, rounded posteriorly, completely covering the embolus; with a long anterior spur curved ventrally at tip (Fig. 409). The large, conspicuous conductor has two parts, one rounded at its tip, the other bearing two irregular points. The embolic spiral is moderately wide, formed by a very slender whip-like duct. The female is unknown.

Natural History. Göldi, 1892, reports finding the species in virgin forest within several days travel of São Eduardo [Santo Eduardo] on the Itabapana, border river between the provinces Rio de Janeiro and Espírito Santo. This probably should be the type locality.

Distribution. Southern Brazil; Map 12.

Records. Brazil. Minas Gerais: Caraça, ♂ (E. Gounelle, MNHN). *São Paulo:* Mata do Governo, Inst. Botanica, São Paulo, March 4, 1959, ♂ (L. Lane). *Santa Catarina:* Nova Teutonia, lat 27°11′, long 52°23′, 1930-1940, ♂ (F. Paumann, SMF).

REFERENCES

Archer, A. F.
1946. The Theridiidae or comb-footed spiders of Alabama. Paper Alabama Mus. Nat. Hist., no. 22, pp. 1-67.

Bonnet, P.
1955. Bibliographia Araneorum, Toulouse, vol. 2, pt. 1, pp. 1-918.

Exline, Harriet
1945. Spiders of the genus *Conopistha* (Theridiidae, Conopisthinae) from northwestern Peru and Ecuador. Ann. Ent. Soc. America, vol. 38, pp. 505-528.

Hentz, N.
1875. The spiders of the United States. Boston, 171 pp.

Lamore, D. H.
1958. The jumping spider *Phidippus audax* Hentz and the spider *Conopistha trigona* Hentz as predators of the basilica spider *Allepeira lemniscata* Walckenaer in Maryland. Proc. Ent. Soc. Washington, vol. 60, p. 286.

Roewer, C. Fr.
1942. Katalog der Araneae. Bremen, vol. 1, 1040 pp.; 1955, *op. cit.*, Brussels, vol. 2b, pp. 927-1751.

Simon, E.
1893. Histoire Naturelle des Araignées. Paris, 1084 pp.

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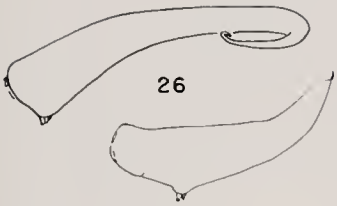
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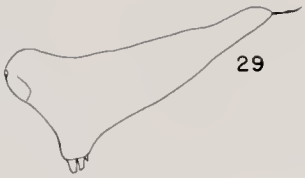
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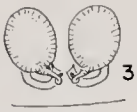
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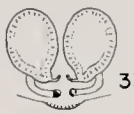
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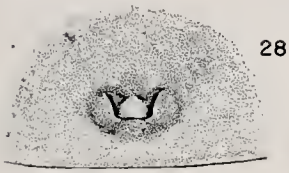
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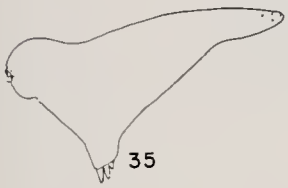
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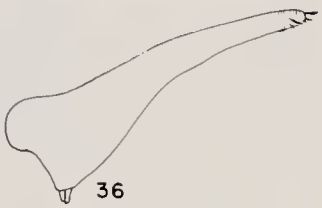
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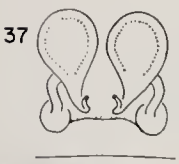
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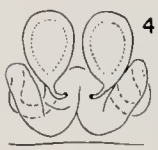
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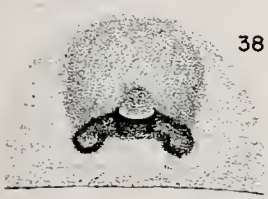
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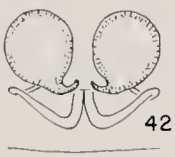
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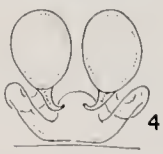
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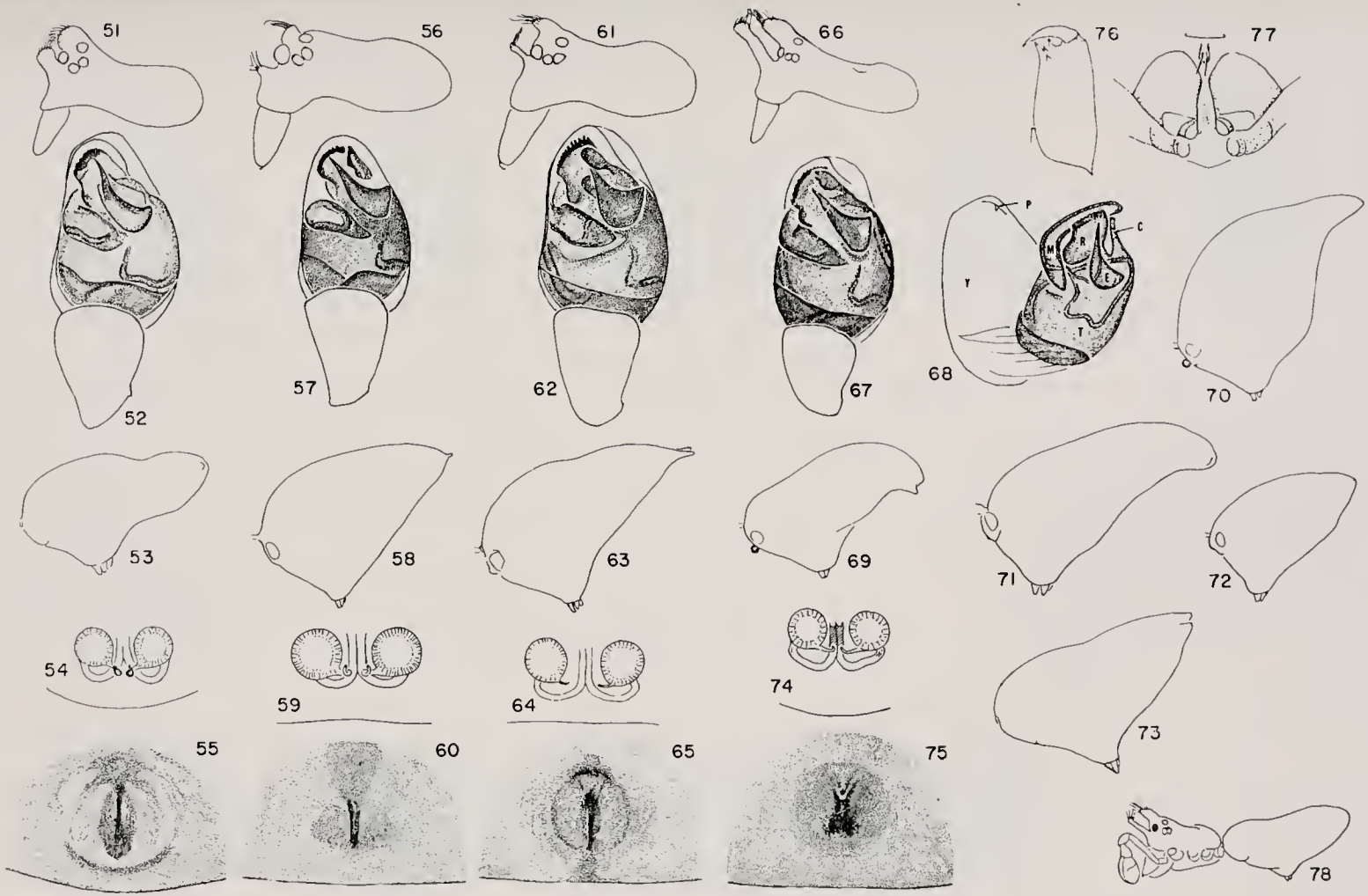
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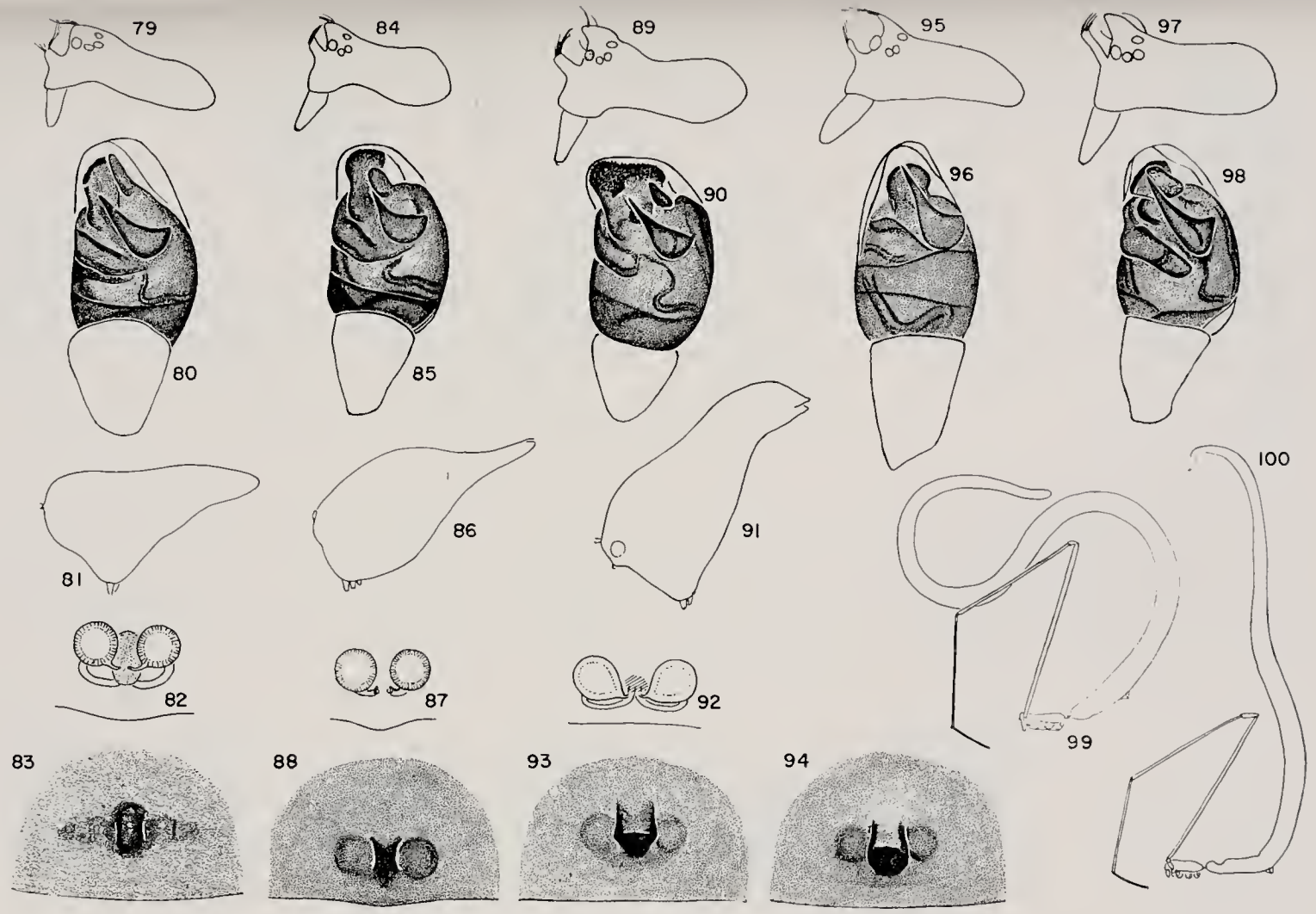
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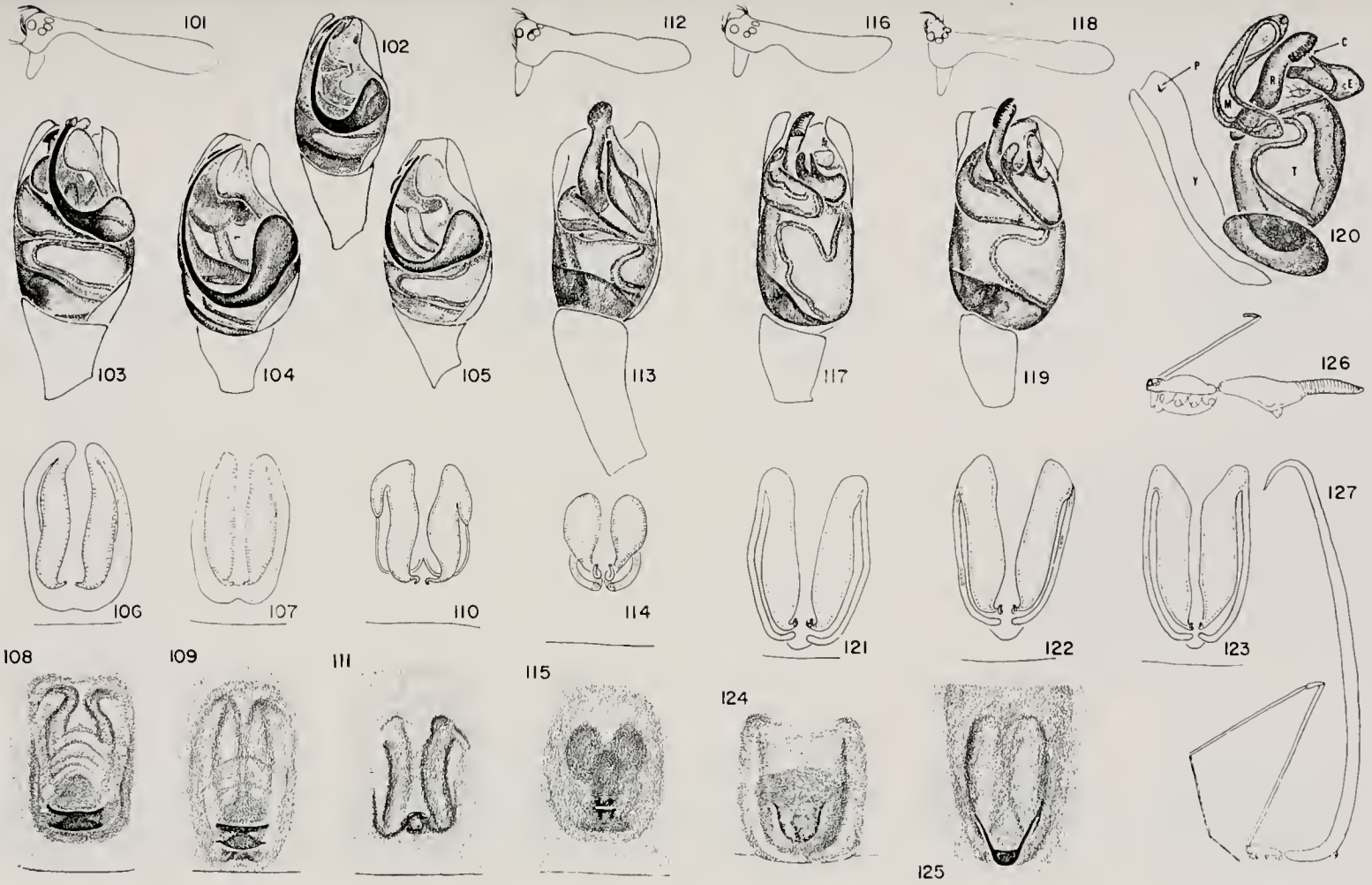
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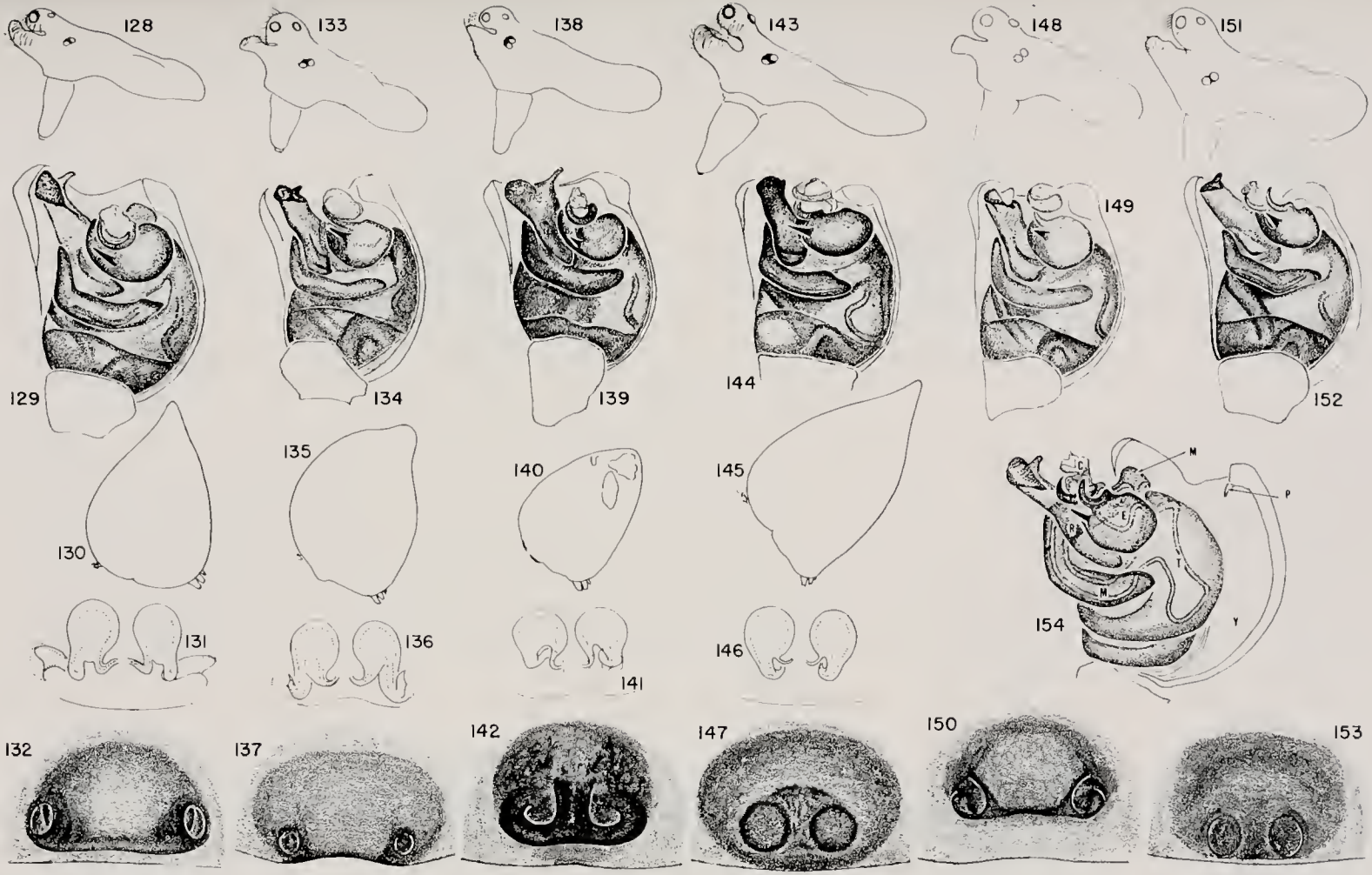
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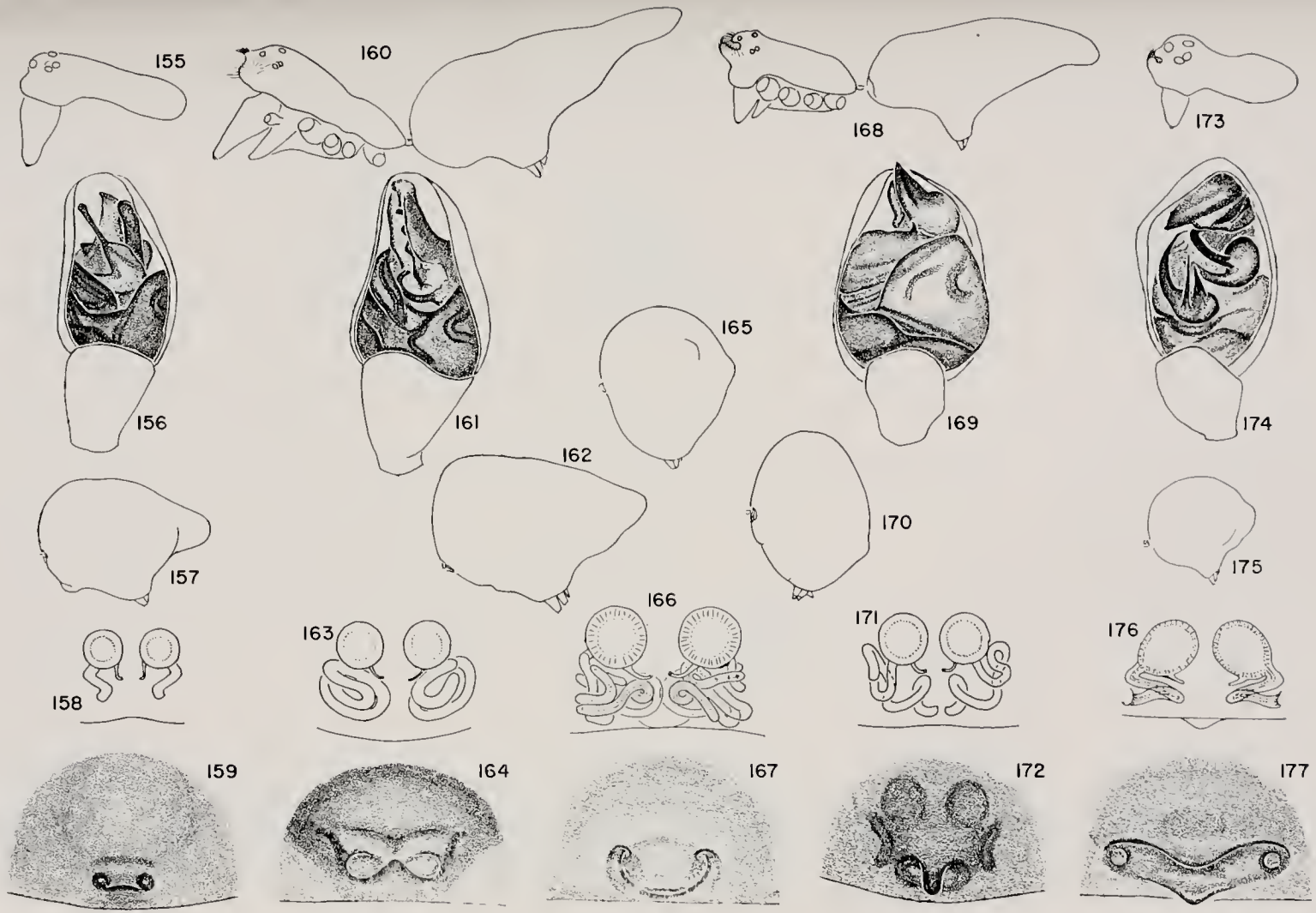
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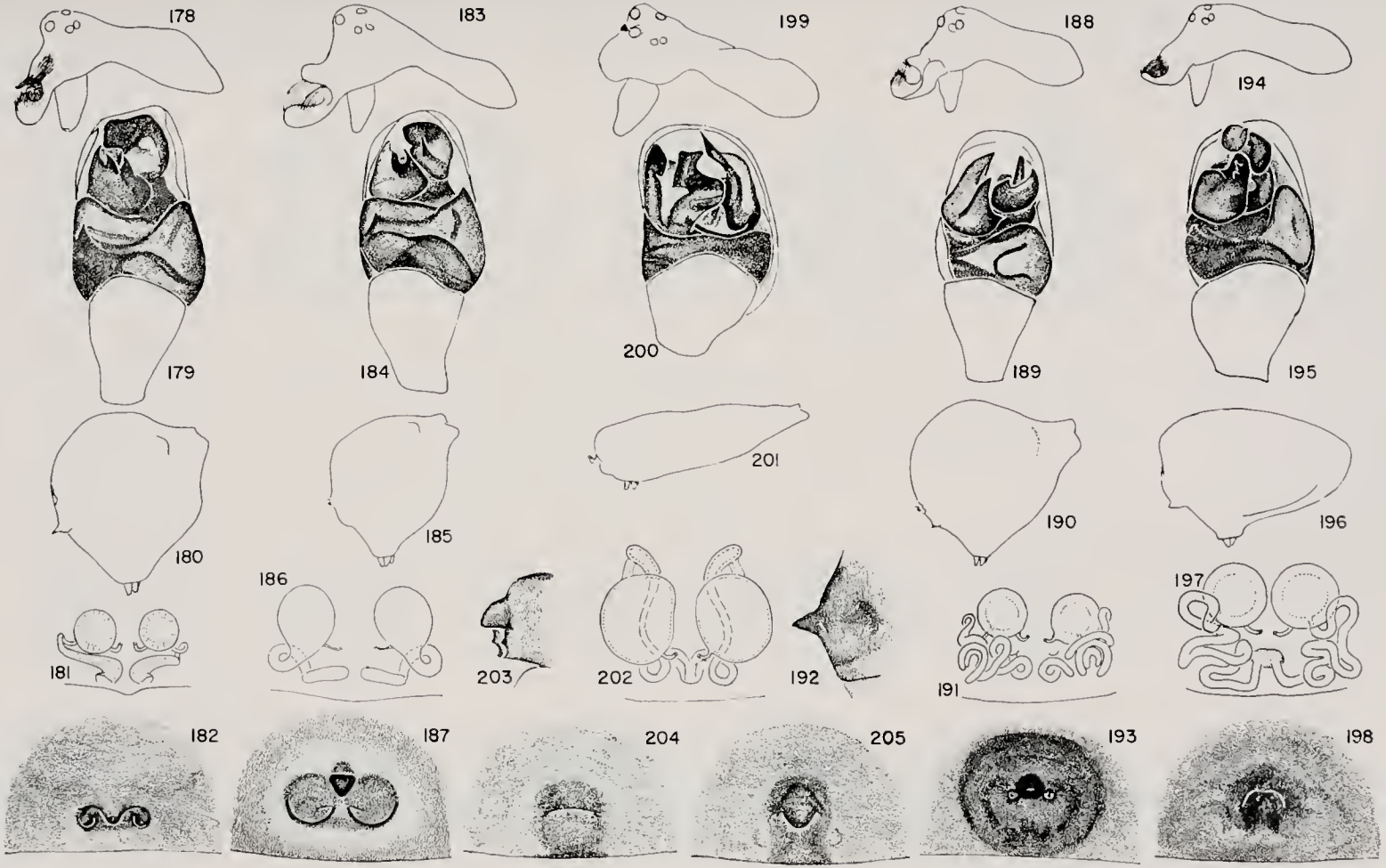
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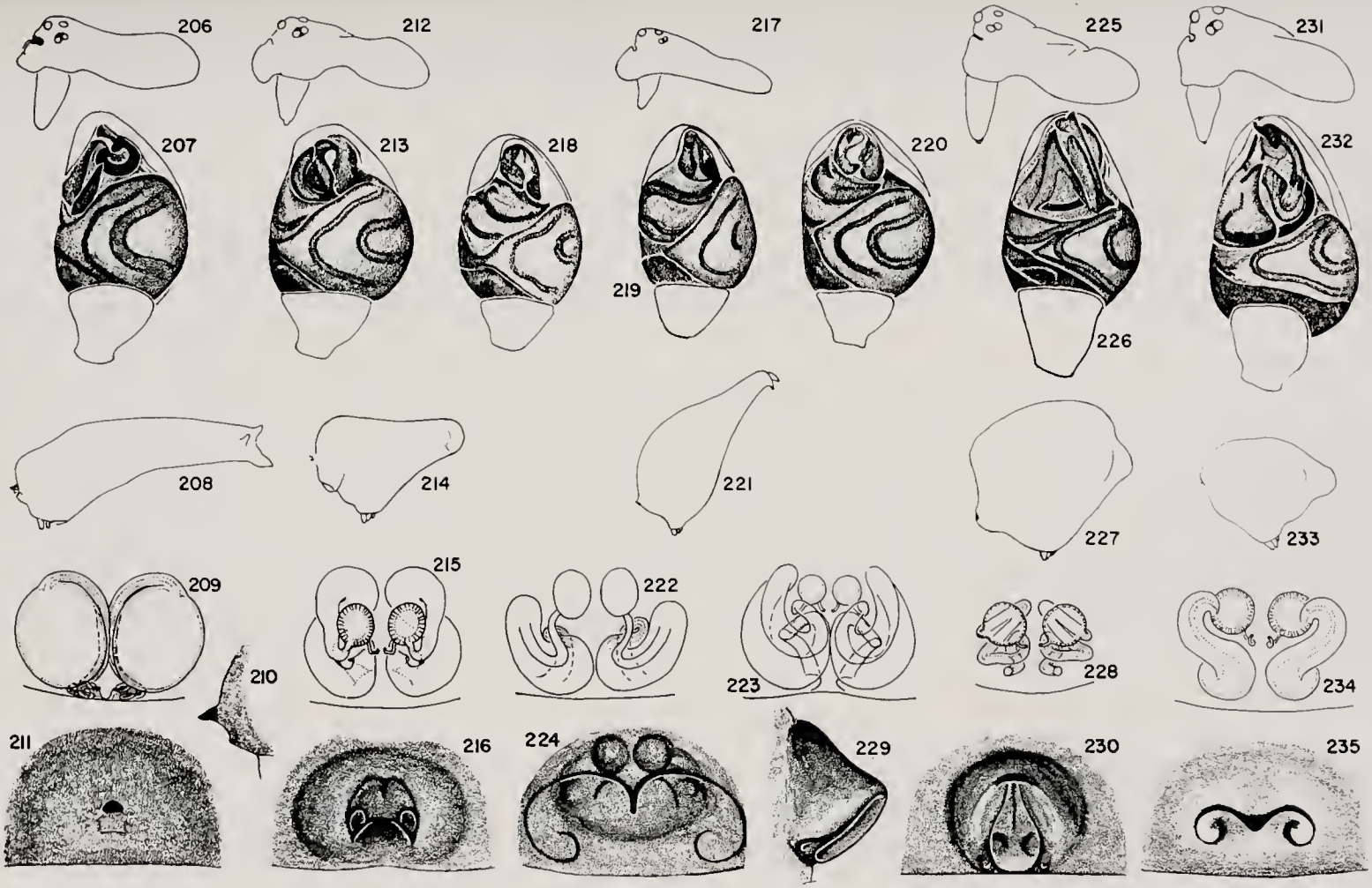
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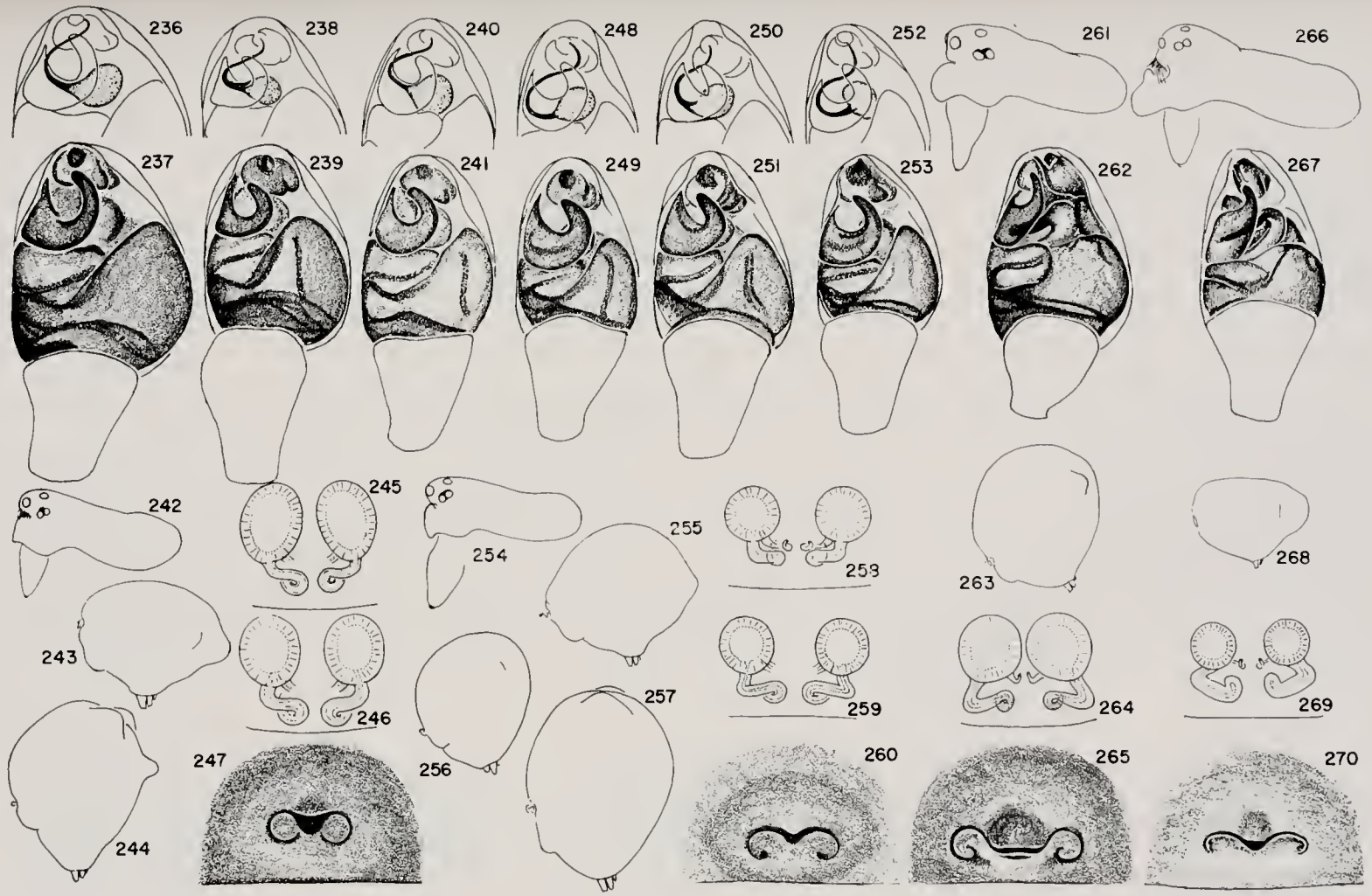
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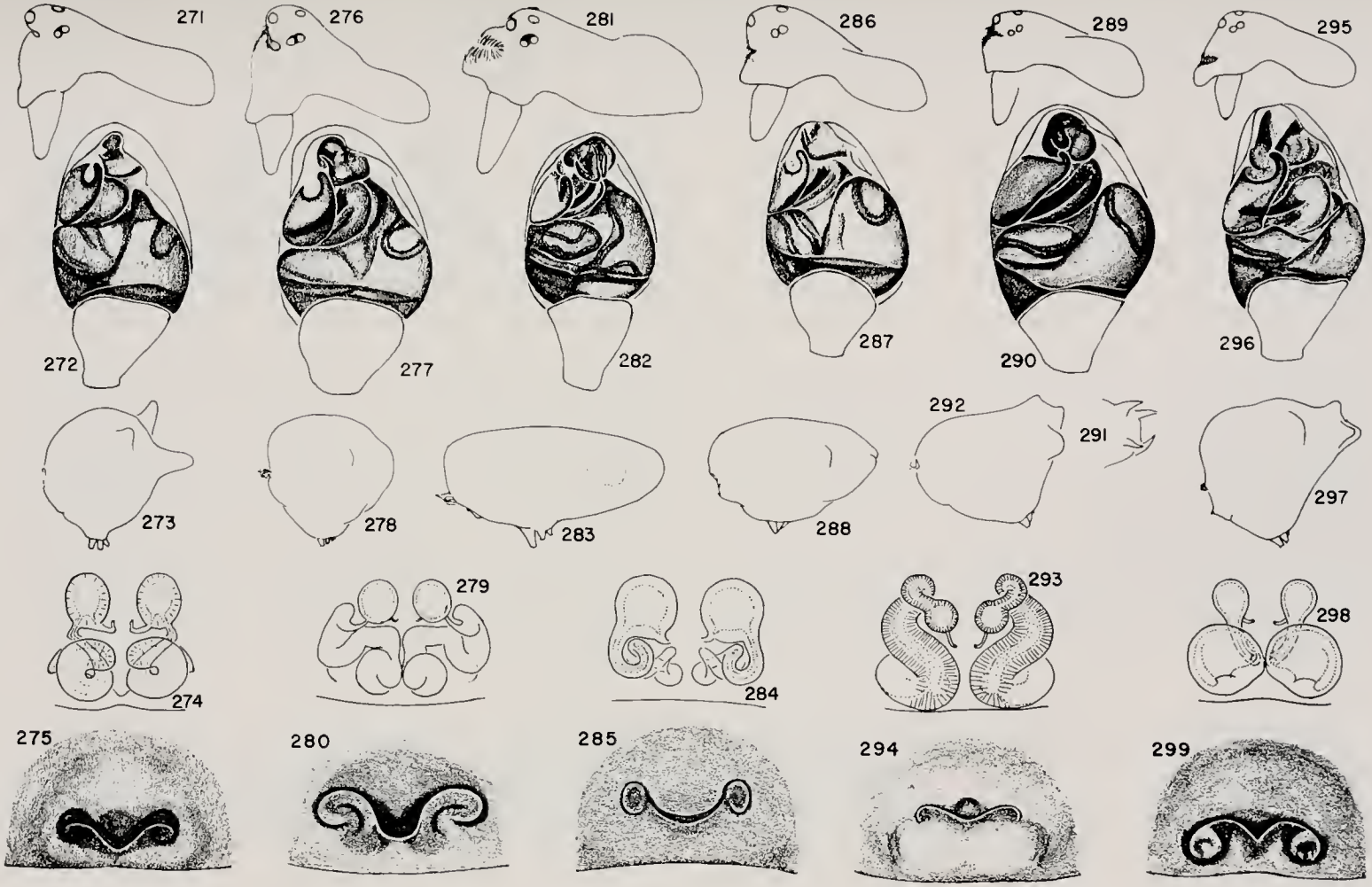
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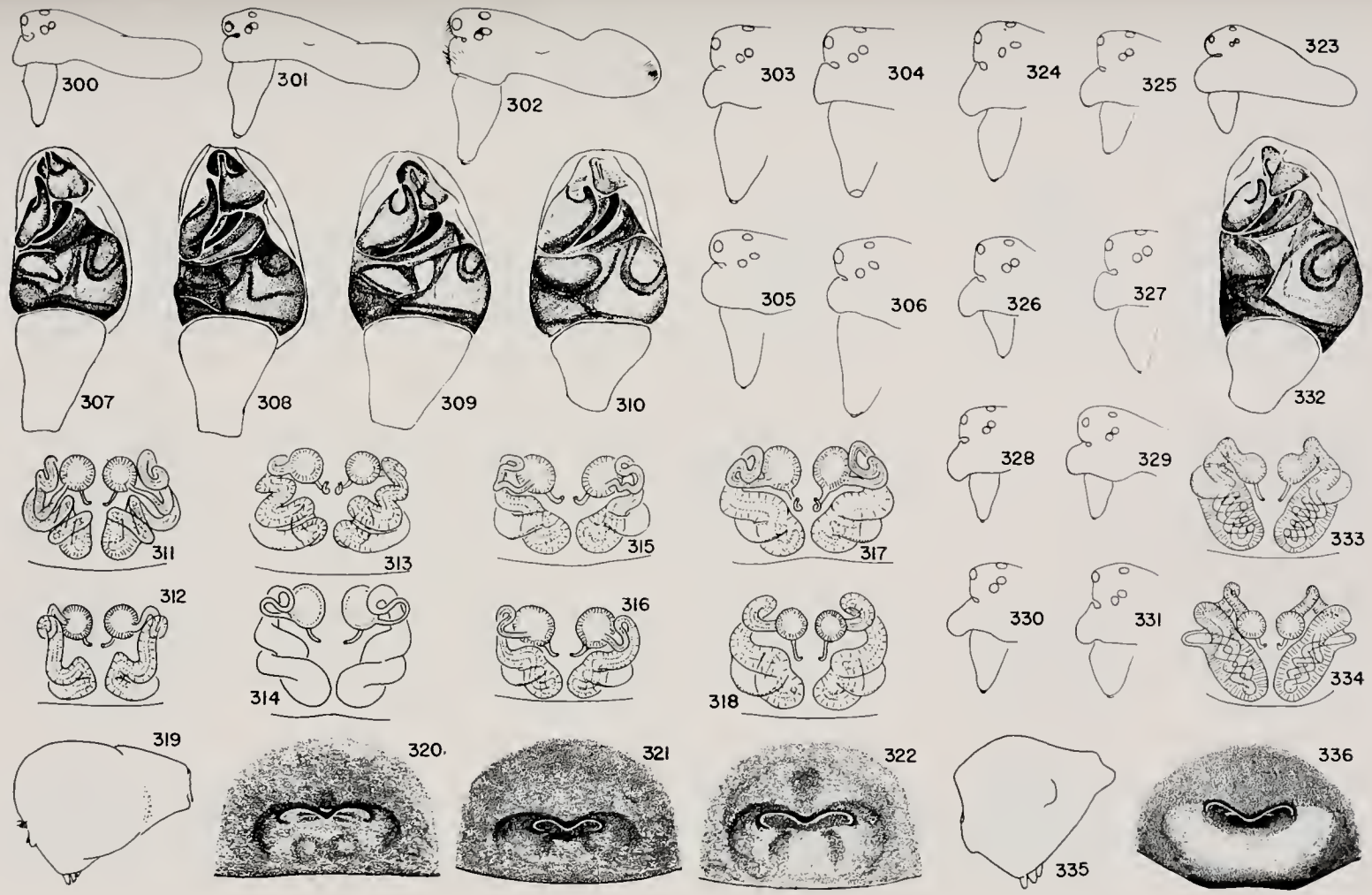
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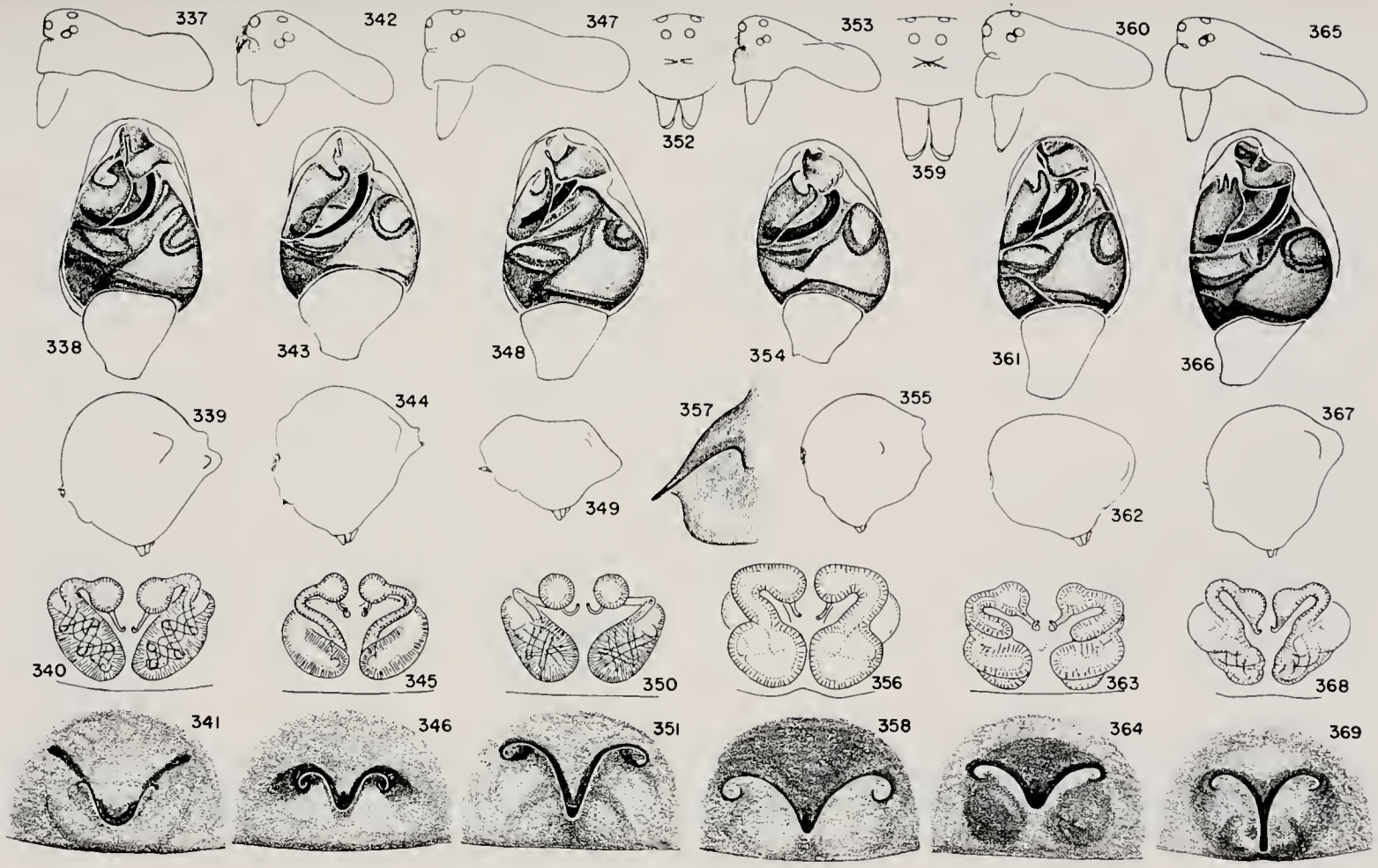
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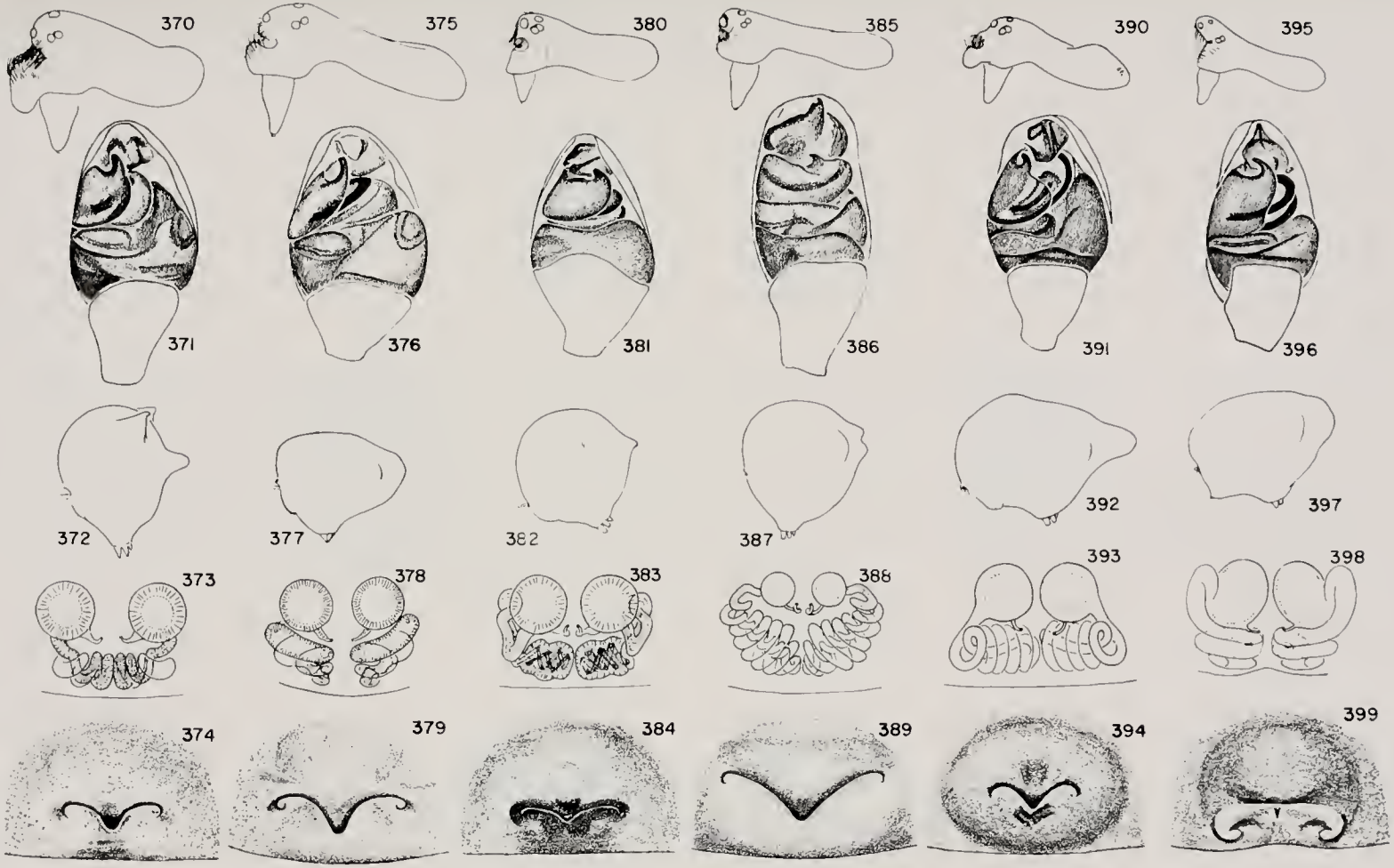
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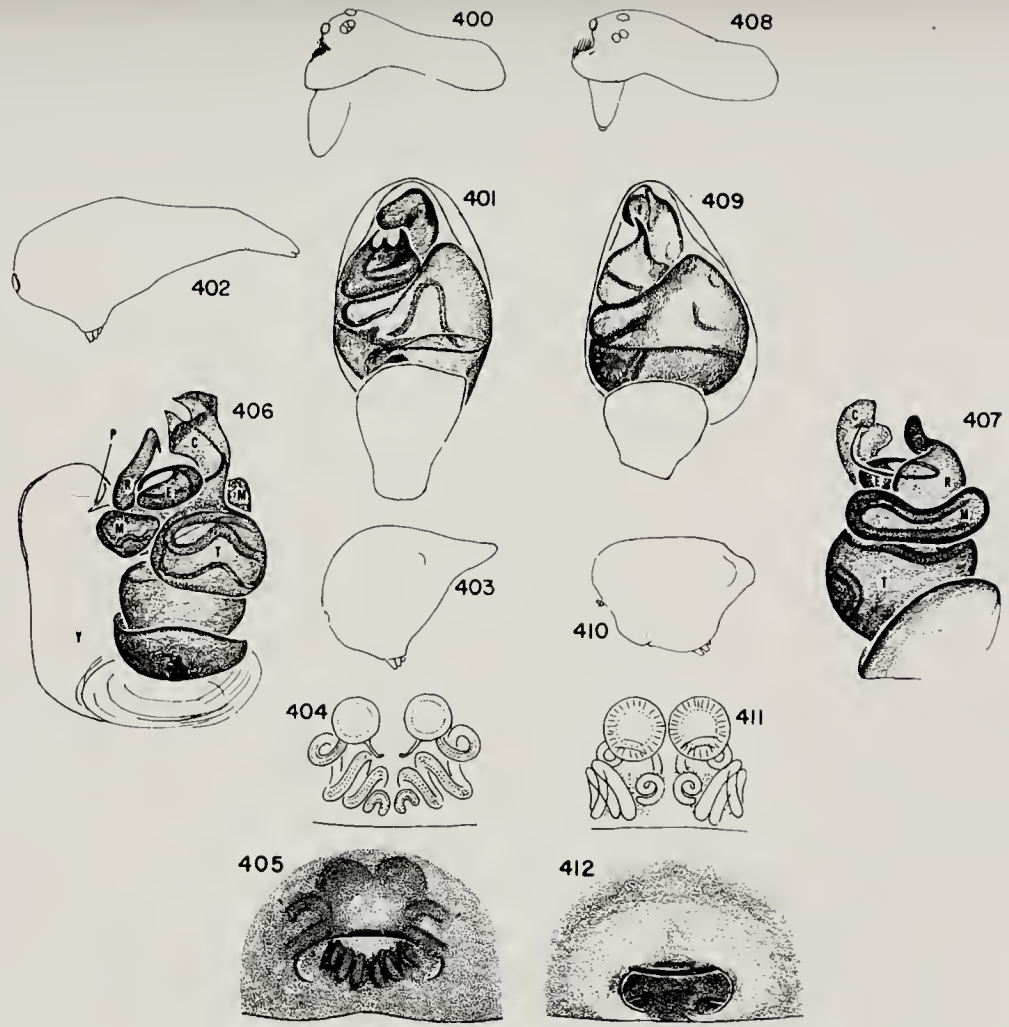
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SCOLOPOPHOROUS ORGANS IN THE PTEROTHORAX AND ABDOMEN OF *GELASTOCORIS OCULATUS* (FABRICIUS) (HEMIPTERA-HETEROPTERA)

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No. 3 — *Scolopophorous Organs in the Pterothorax and Abdomen of Gelastocoris oculatus (Fabricius) (Hemiptera-Heteroptera)*

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INTRODUCTION

Scolopophorous organs located on the body, as opposed to those on the appendages, are widely distributed among the orders of insects. These organs, which are especially common in immature insects, are also found in adult Lepidoptera, Hymenoptera, Odonata, Diptera, Homoptera, and Heteroptera (Eggers, '28). In some insects they may be highly complex, each organ consisting of a large number of strand-like sensilla. In this work there will be no attempt to review the extensive literature on these organs in insects other than the Heteroptera; however, it may be noted here that there have been numerous recent papers on their structure, most notably that of Gray ('60) on the electron microscopy of the scolopophorous organs of *Locusta*.

Among the Heteroptera, scolopophorous organs have previously been reported only in representatives of the Hydrocorisae or totally aquatic bugs. Most earlier workers observed them only in the mesothorax; these paired mesothoracic organs were described in the Corixidae (Hagemann, '10; Eggers, '28; Wotzel, '33; Schaller, '51), Pleidae (Wefelscheid, '12; Eggers, '28; Wotzel, '33), Notonectidae (Wefelscheid, '12; Eggers, '28; Wotzel, '33), Naucoridae (Wefelscheid, '12; Eggers, '28; Wotzel, '33) and Nepidae (Wotzel, '33). Similar organs on the metathorax were reported by Wotzel ('33) in the Naucoridae and Nepidae.

A recent survey by Larsén ('57) has revealed that in the Hydrocorisae scolopophorous organs occur not only in the mesothorax and metathorax but also in the first and sometimes the second abdominal segment. That author found discolopodial organs, each consisting of two sensilla, in the pterothoraxes and first abdominal segments of *Nepa* and *Ranatra* (Nepidae), *Naucoris* (Naucoridae), *Aphelocheirus* (Aphelocheiridae), *Notonecta* (Notonectidae), and *Corixa* (Corixidae). He also discovered monoscolopodial organs, each composed of a single sensillum, in the first abdominal segments of *Corixa* and *Aphelocheirus* and in the second abdominal segment of *Aphelocheirus*. Each segment containing scolopophorous organs possesses a pair of them, one lying on either side. Larsén criticized the theory, held by most previous workers, that the heteropteran scolopophorous organs are tympanal organs, and suggested that they may be equilibrium perceptors.

It now appears that scolopophorous organs in the Heteroptera are not limited to the Hydrocorisae. The present author has recently been studying the morphology of the shore-dwelling bug *Gelastocoris oculatus* (Fabricius), a representative of the family Gelastocoridae. This family is considered by China ('55) and other workers to have arisen as an early offshoot of the ancestral Hydrocorisae, and previous studies of the head (Parsons, '59), thorax (Parsons, '60a) and nervous system (Parsons, '60b) of *Gelastocoris* have supported this theory. *Gelastocoris* possesses discolopodial organs in the mesothorax, the metathorax, and the first abdominal segment, and a monoscolopodial organ, similar to that of *Aphelocheirus* or *Corixa*, in the first abdominal segment. In addition, a discolopodial organ occurs in the second abdominal segment; to the author's knowledge, this has not been previously observed in any other heteropteran.

MATERIALS AND METHODS

Both the gross and the histological morphology of the gelastocorid scolopophorous organs were studied. Dissections were made upon a large number of adult *Gelastocoris* preserved in aqueous Bouin's, alcoholic Bouin's, Kahle's, F.A.A., or 10% formalin. The insects were dissected in 80% alcohol under a stereoscopic microscope. For histological study, seven gelastocorids were serially sectioned, at 7μ, by the paraffin method. These individuals were killed just after the adult moult, while their exoskeletons were still soft. They were preserved in aqueous or alcoholic Bouin's, F.A.A., or 10% formalin, and were prepared for sectioning by means of the Peterfi method. Both transverse and frontal sections, stained with Mallory's triple connective tissue stain, were employed.

OBSERVATIONS

Gross Morphology

The scolopophorous organs of *Gelastocoris* consist of one (as in the *monoscolopodial organ*[1] of the first abdominal segment) or two (as in the other organs) sensory *sensilla* or *scolopodia*, whose histological appearance will be described later. In the *discolopodial organs* the two sensilla are united into a common strand. The distal end of the scolopophorous organ may attach to a membrane on the body wall, as in the thorax and the first abdominal segment, or it may terminate upon an undifferentiated part of the exoskeleton, as in the second abdominal segment. Its proximal end, where it joins a sensory nerve, may be closely associated with a trachea (as in the thoracic organs) or with the endoskeleton (as in the first abdominal segment), or it may lie freely within the body cavity (as in the second abdominal segment). In the following discussion the scolopophorous organs of each segment will be considered separately.

Mesothoracic scolopophorous organ. The distal end of the mesothoracic organ attaches to a membrane which lies on the lateral mesothoracic body wall within the air space between the wings and the pleuron (Fig. 1, *SM 2*). Posteriorly and posterodorsally the membrane is bordered by the postalar bridge (*B 2*), which is formed by the union of the mesothoracic postnotum and

1 The terminology in the present paper is that customarily used for the scolopophorous organs of Heteroptera; somewhat different terms have been used by other authors for other groups of insects.

epimeron. Ventrally it borders on the epimeron (*E 2*), while anteriorly and anterodorsally it is continuous with the membrane of the forewing (*FW*). Just anterior to it lies the irregularly shaped subalare (*S 2*). Larsén ('57) has described a similar connection of the sensory membrane with the subalar membrane

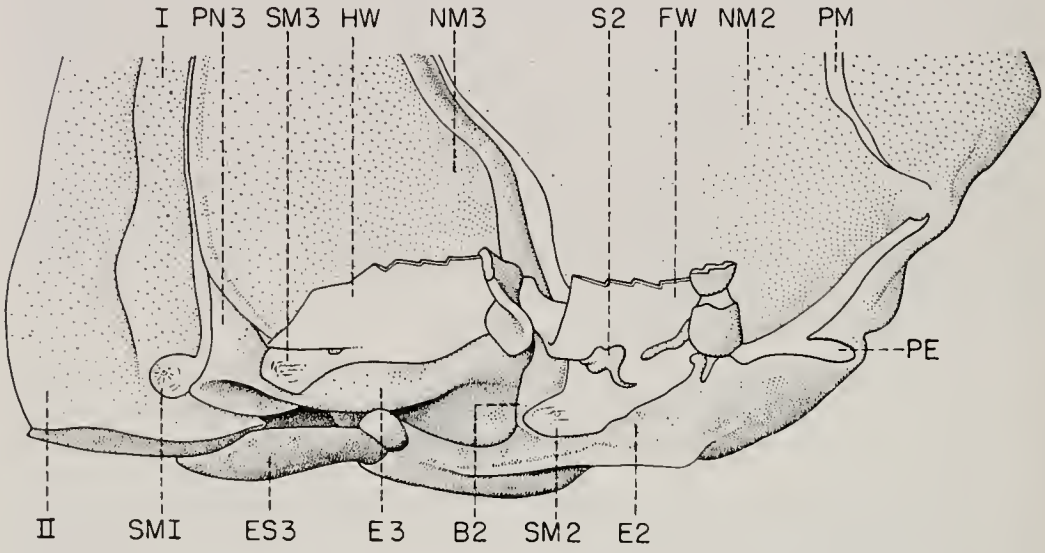

Fig. 1. Dorsolateral view of the right side of the pterothorax and the first two abdominal segments, showing the location of the sensory membranes of the discolopodial organs. The wings, the prothorax, and the posterior part of the abdomen have been cut off. Membranous areas are unstippled. X35.

in *Naucoris* and *Notonecta* and possibly in *Plea;* in those insects he thinks it possible, but not probable, that the motion of the wing may affect the organ. In the other Hydrocorisae examined by him the sensory membrane is separated from the wing membrane by a sclerotized ring.

The sensory membrane in *Gelastocoris* is separated from the external opening of the metathoracic spiracle, which lies ventral and medial to it, by a longitudinal ridge on the inner surface of the epimeron. Larsén ('57) has described a similar separation of the membrane and the spiracle in *Nepa, Naucoris, Ranatra,* and *Aphelocheirus;* he found no such separation in *Notonecta* or *Corixa.*

The appearance of the sensory membrane (which Hamilton, '31, apparently mistook for the metathoracic spiracle in *Nepa*) is shown in Figure 2A. The point of attachment of the sense organ on the membrane appears externally as an indistinct,

slightly raised area. This represents the "Höcker" or "Trommelfellkörper" of previous authors. In some specimens a minute dark spot can be observed in the center of this raised area. This spot may be a very small sclerite, similar to those observed by Larsén ('57) in the sensory membranes of many Hydrocorisae.

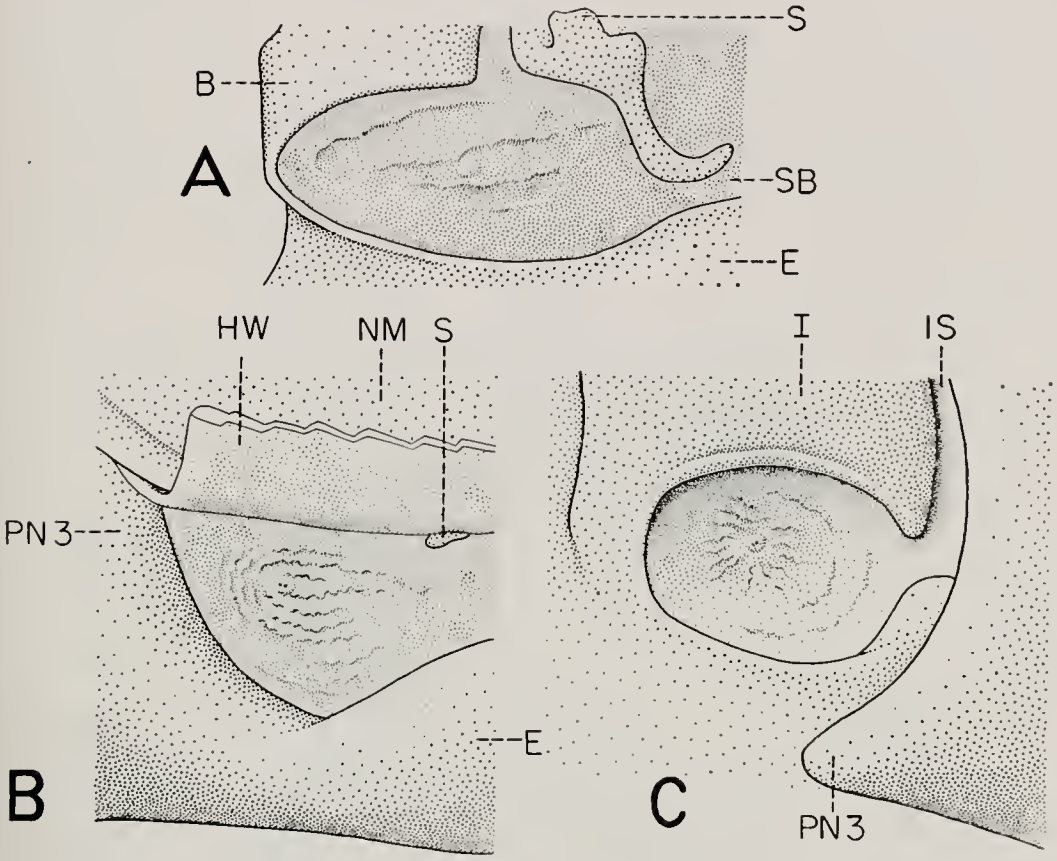

Fig. 2. External appearance of the sensory membranes of the right side of the body. Heavy stippling indicates heavily sclerotized structures; light stippling indicates membranous regions. A, Mesothoracic sensory membrane. B, Metathoracic sensory membrane. C, First abdominal sensory membrane.

In the histological preparations, however, the raised area appeared more as a thickening of the membrane than as a definite sclerite. A few indistinct longitudinal folds may be observed in the membrane, but the folding is not as pronounced as in the mesothoracic sensory membranes of the Hydrocorisae described by Wotzel ('33) and Larsén ('57).

From its point of attachment on the membrane the mesothoracic scolopophorous organ (*D 2*) extends medially and somewhat posteriorly into the body cavity, beneath the postnotum (Figs.

3, 4). Proximally its base attaches to a trachea (*DT 2*); a similar connection of the base of the mesothoracic scolopophorous organ with the tracheal system has been noted by Larsén ('57) in the Hydrocorisae. Since the thoracic tracheal system of *Gelastocoris* shows some peculiarities, it will here be treated in some detail.

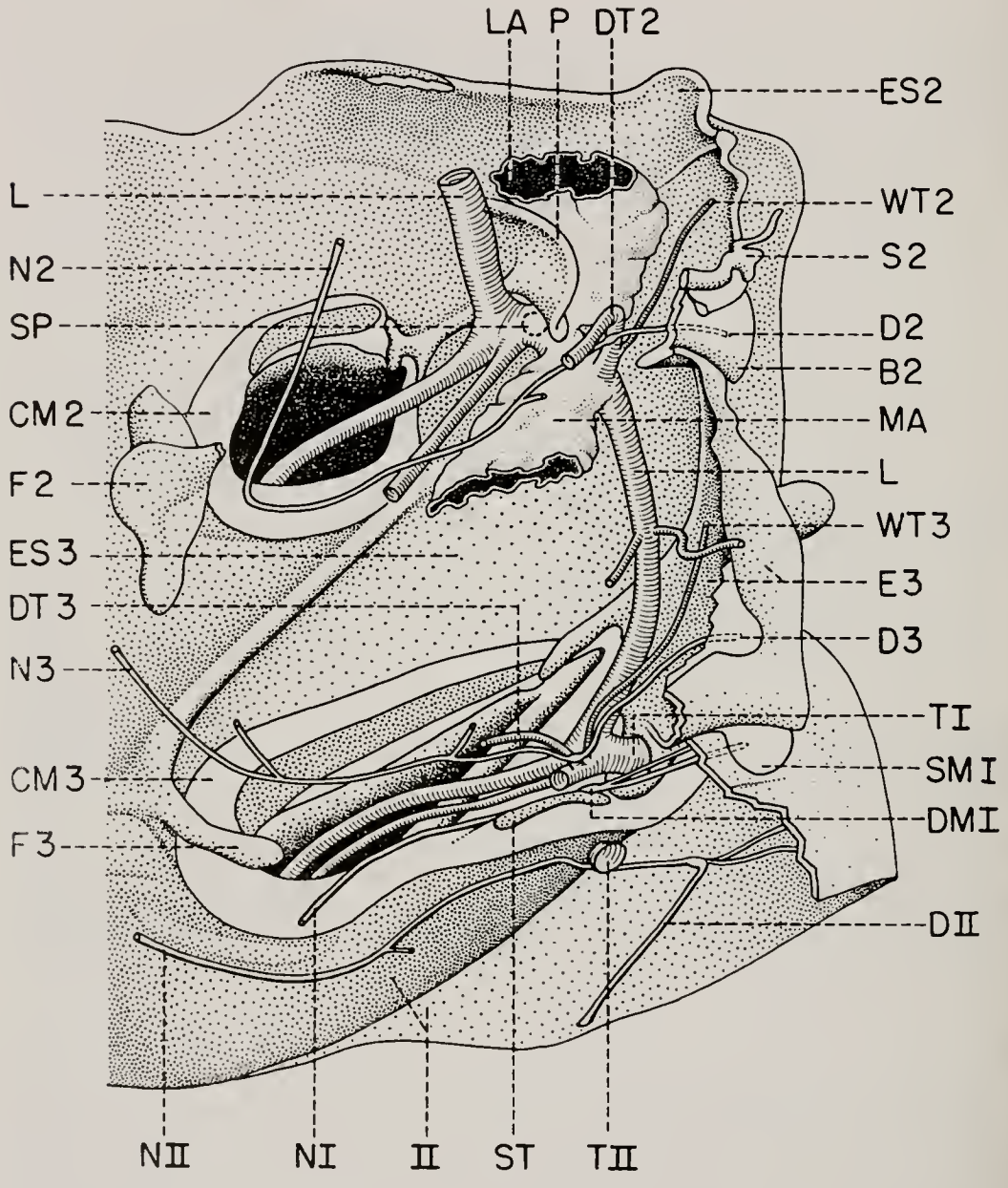

Fig. 3. Inner surface of the pterothorax and first two abdominal segments, right side, with the terga, wings, and muscles removed to reveal the scolopophorous organs, air sacs, and major tracheae. Membranous regions and cut edges are unstippled. Most of the tracheae have been cut off near their bases, and the distal parts of the air sacs have been removed. X40.

The *metathoracic spiracle* (Fig. 3, *SP*) lies in the ventrolateral part of the body, at the boundary between the mesothorax and the metathorax. It was incorrectly termed the "mesothoracic spiracle" by both Brocher ('09) and Maulik ('16). Its external opening is overlapped and concealed by the extensive posterior lobe of the mesothoracic epimeron, which has been described in a previous paper (Parsons, '60a). A large, longitudinal *lateral tracheal trunk* (Figs. 3, 4, *L*) ("spiracular trunk trachea" of Hamilton, '31, and Presswalla and George, '35; "Längstracheenstamm" of Larsén, '57) joins the metathoracic spiracle with the more posterior *first abdominal spiracle* ("metathoracic spiracle"

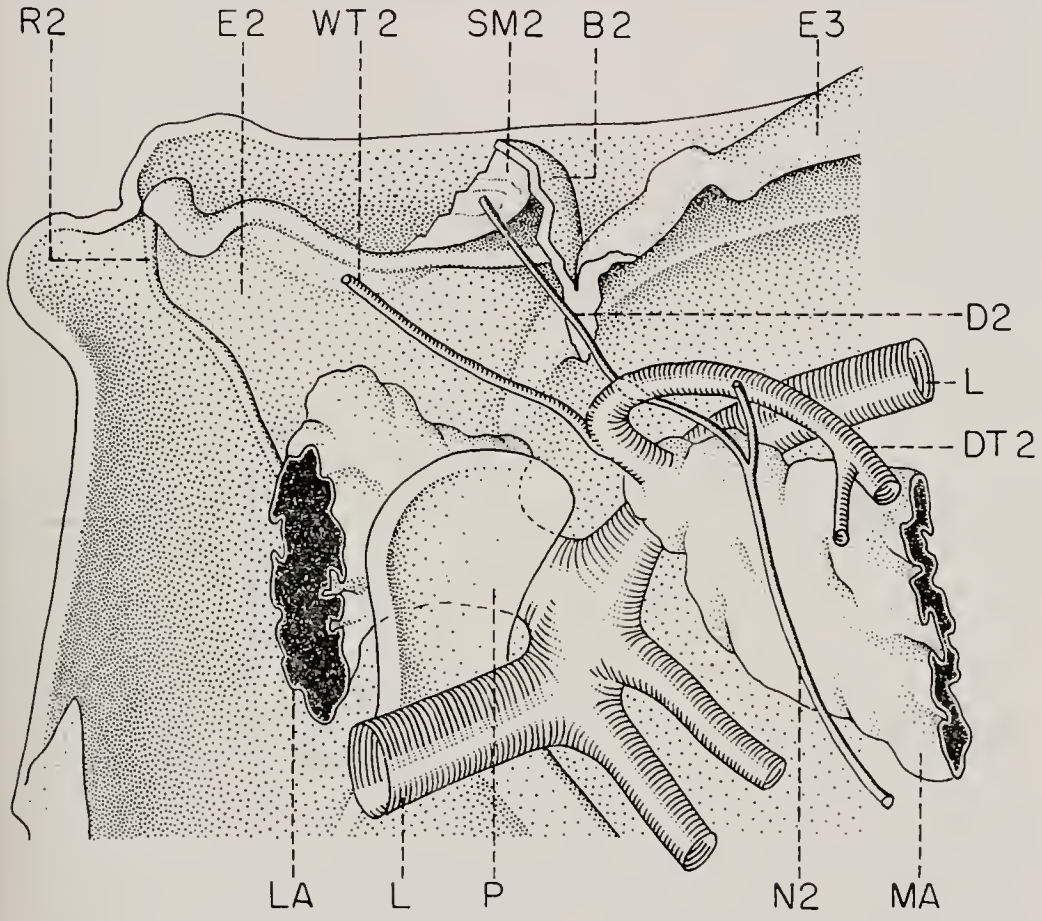

Fig. 4. Dorsal view of the right side of the mesothorax and part of the metathorax, with wings, terga, and muscles removed. Part of the mesothoracic postalar bridge has been cut away to reveal the mesothoracic sensory membrane. The metathoracic spiracle and spiracular trachea are here concealed by the lateral tracheal trunk, which lies dorsal to them. Only the bases of the tracheae and air sacs are shown. Anterior region is shown at the left, posterior region at the right. X65.

of Brocher, '09, and Maulik, '16). Anteriorly, the lateral tracheal trunk extends medial to the mesothoracic pleural apophysis (Figs. 3, 4, *P*) and joins the *mesothoracic spiracle* ("prothoracic spiracle" of Brocher, '09, and Maulik, '16), which lies between the prothorax and the mesothorax.

A very short *spiracular trachea* connects the metathoracic spiracle with the lateral tracheal trunk and also sends off tracheae to the mesothoracic leg and to the sternal area. From the lateral tracheal trunk, in the region where it unites with the spiracular trachea, arise two large *air sacs* (Figs. 3, 4, *LA* and *MA*) with very thin, folded walls. These sacs are very delicate and are easily torn in dissections. Histological preparations reveal that they are composed of a folded layer of small cuboidal cells with a cuticular intima in which taenidia are either very faint or absent. The air sacs are broadly joined to the lateral tracheal trunk and do not arise from a constricted tracheal stalk as do the "Tracheenblasen" of many of the Hydrocorisae described by Larsén ('57). They were not observed in histological preparations of a nymph which had just moulted from the fourth to the fifth instar. These sacs were collapsed in all the specimens examined, and were never filled with air.

The *lateral air sac* (Figs. 3, 4, *LA*) arises just lateral to the metathoracic spiracle and extends forward between the body wall and the pleural apophysis, adhering closely to the latter. Anterior to the pleural apophysis it turns medially and becomes associated with one of the indirect flight muscles, *M. mesonoti secundus*, to which it sends many fine tracheoles. The lateral and medial walls of the sac are closely apposed. Air sacs with a similar position in the body have been described in many Hydrocorisae. The lateral air sac of *Gelastocoris* resembles the "bulbous trachea of the mesothorax" of *Sphaerodema* (Presswalla and George, '35) and is probably homologous with the "vordere Tracheenblase" described by Larsén ('57) in several aquatic bugs. In the majority of Hydrocorisae a lateral air sac lies close to the membrane of the mesothoracic scolopophorous organ; this has been observed in *Notonecta* (Wefelscheid, '12; Wotzel, '33; Larsén, '57), *Naucoris* (Wotzel, '33; Larsén, '57), *Nepa* (Wotzel, '33; Larsén, '57), *Ranatra* (Larsén, '57), and *Belostoma* (Larsén, '57). The association of the air sac and the sensory membrane is particularly close in the Corixidae (Hagemann, '10; Eggers, '28; Wotzel, '33; Larsén, '57). In *Gelastocoris,* however, the lateral air sac lies at a considerably greater

distance from the sensory membrane than in any of the Hydrocorisae, and does not appear to be in any way associated with it. Larsén ('57) noted that in many of the aquatic bugs the lateral wall of the "vordere Tracheenblase" is more delicate than the medial wall. In *Gelastocoris,* however, no histological difference was noted between the two walls.

From the lateral tracheal trunk just posterior to the metathoracic spiracle arises a second sac, the *medial air sac* (Figs. 3, 4, *MA*), which extends posteromedially between the mesothorax and the metathorax. It passes posterior to the ventral process of the second thoracic phragma. The medial air sac lies between and sends fine tracheoles to the tergal remotor muscle of the middle leg (*M. noto-coxalis*) and the tergal depressor muscle of the metathoracic trochanter (*M. noto-trochanteralis*). Like the lateral air sac, its walls are closely apposed, especially in the region behind *M. noto-coxalis;* in dissections it appears as a broad dorso-ventral sheet separating that muscle from *M. noto-trochanteralis.* Medially it becomes associated with and sends fine tracheoles to the dorsal longitudinal flight muscles of the mesothorax, *Mm. mesonoti primus et secundus.*

Arising from the dorsal wall of the medial air sac, just where the latter joins the lateral tracheal trunk, is a medium-sized *dorsal trachea* (Figs. 3, 4, *DT 2*). This trachea extends dorsally and then turns medially, running along the region beneath the mesothoracic postnotum and just anterior to the second thoracic phragma. From its base it sends off a fine trachea (*WT 2*) to the wing. The base of the mesothoracic scolopophorous organ attaches to the posterior surface of this dorsal trachea, dorsal to the fine trachea which runs to the wing.

In both its position and its association with the mesothoracic scolopophorous organ, the dorsal trachea corresponds to the "Tracheenast" described by Wotzel ('33) in the mesothorax of *Notonecta.* Larsén ('57) has described a "hintere Tracheenblase," in the mesothoraxes of many Hydrocorisae, which arises from the "Längstracheenstamm" in the same region as does the dorsal trachea of *Gelastocoris,* and which, similarly, lies beneath the postnotum. In *Notonecta, Ranatra,* and *Nepa,* the mesothoracic scolopophorous organ attaches to the tracheal stalk of this posterior air sac. These similarities make it appear probable that the dorsal trachea of *Gelastocoris,* although not an air sac, is homologous with the "hintere Tracheenblase" of the Hydrocorisae. In *Aphelocheirus aestivalis,* according to Larsén ('57),

a "hintere Tracheenblase" is present in the nymph but appears in the adult as a trachea which lacks taenidia. This adult trachea lies in the same position as does the dorsal trachea of *Gelastocoris* and, similarly, serves as a point of attachment for the base of the mesothoracic scolopophorous organ.

The medial air sac of *Gelastocoris* resembles, in its position posterior to the ventral process of the second phragma and in its association with the dorsal longitudinal muscles of the mesothorax, the large trachea "Tr" of *Nepa* and *Ranatra* which is figured by Larsén ('57; his fig. 9). It also occupies the same position as the sac-like trachea which supplies the dorsal longitudinal muscles of *Notonecta* and which Larsén ('57) shows in his figure 25. The trachea to which the mesothoracic scolopophorous organ attaches (the dorsal trachea of *Gelastocoris* and the "hintere Tracheenblase" of *Notonecta*) arises from the base of the sac-like trachea of *Notonecta* and from the base of the medial air sac of *Gelastocoris*.

The mesothoracic scolopophorous organ is innervated by a branch of *nervus mesothoracicus primus* (Figs. 3, 4, *N 2*). As has been described in an earlier paper (Parsons, '60b), this first mesothoracic nerve sends a ramus to the dorsal longitudinal flight muscles, *Mm. mesonoti primus et secundus*. From the base of this ramus a branch extends posteriorly, passing medial to the promotor muscle of the middle leg, *M. noto-trochantinalis*, and then turning dorsolaterally, behind the remotor muscle of the leg, *M. noto-coxalis*. This nerve sends off a fine branch to the notum and then runs laterally, alongside (and often adhering to) the dorsal trachea. Near the base of the latter the nerve joins the proximal end of the scolopophorous organ, at the point at which the organ is attached to the posterior surface of the dorsal trachea (Figs. 3, 4, 11).

Metathoracic scolopophorous organ. Like the scolopophorous organ of the mesothorax, that of the metathorax attaches distally to a membrane (*SM 3*) lying within the subalar air space (Fig. 1). This membrane is bordered posteriorly by the metathoracic postnotum (*PN 3*) and ventrally by the epimeron (*E 3*). Anteriorly and dorsally it is continuous with the membrane of the hindwing (*HW*); just anterior to it lies the minute subalare (Fig. 2B, *S*). In belostomatids, *Naucoris*, and *Notonecta* the sensory membrane of the metathorax is similiarly continuous with the membrane of the wing; in *Nepa* and *Ranatra*, however, it is separated from the latter by a sclerotized ring (Larsén, '57).

Hamilton ('31) termed this membrane the "false spiracle" in *Nepa*. In *Aphelocheirus* the metathoracic scolopophorous organ lacks a sensory membrane (Larsén, '57).

In most specimens two minute dark spots on the membrane indicate the point of attachment of the scolopophorous organ. Whether or not these are definite sclerites could not be determined. As on the mesothoracic sensory membrane, the point of attachment of the sense organ appears as a small raised area.

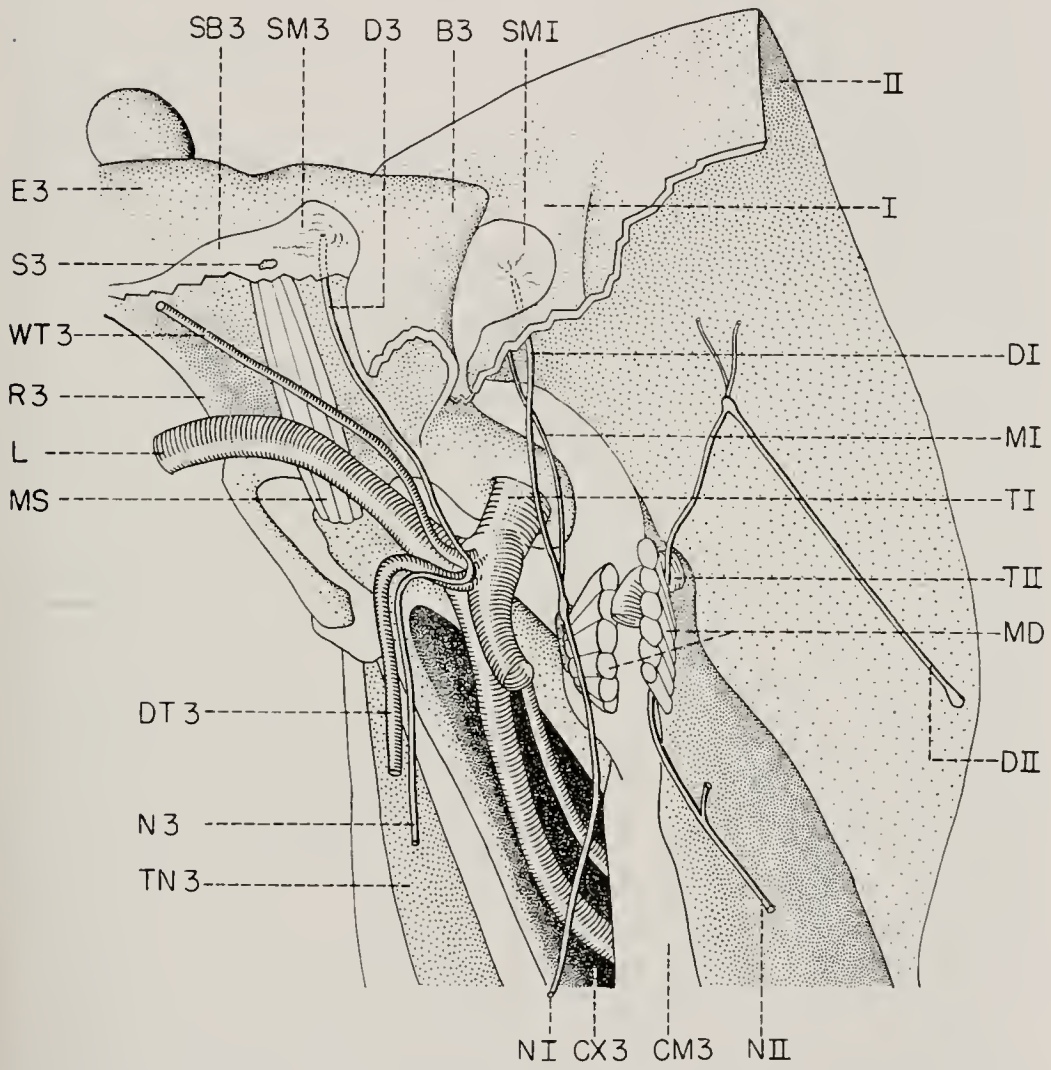

Fig. 5. Dorsal view of the first two abdominal segments and the posterior part of the metathorax, right side, with the terga, the wings, and most of the muscles removed. Membranous areas and cut edges are unstippled. The distal portions of most tracheae and the dorsal parts of the dorsoventral muscles are cut off. Anterior region is shown at the left, posterior region at the right. X65.

Arranged around this point are many finely undulate longitudinal or concentric folds (Fig. 2B). The folds are more conspicuous in the metathoracic sensory membrane than in that of the mesothorax.

From the membrane the scolopophorous organ (Figs. 3, 5, *D 3*) runs medially and somewhat posteriorly to attach, like the mesothoracic organ, on a trachea (*DT 3*). Larsén ('57) reported a similar attachment of the base of the metathoracic sense organ on the tracheal system in most Hydrocorisae (the corixids are exceptions).

In the region of the metathoracic scolopophorous organ of *Gelastocoris* there are no air sacs; this is also true of the aquatic bugs (Larsén, '57). The first abdominal spiracle is surrounded by a sclerotized process of the abdomen which is fused with the metathoracic epimeron (Figs. 3, 5). A short, broad *spiracular trachea* (*TI*) joins the first abdominal spiracle with the lateral tracheal trunk from the metathoracic spiracle. It also sends two tracheae ventrally into the hindleg and, more dorsally, gives rise to a trachea which passes medially into the region between the thorax and the abdomen. From the dorsal part of the area in which the latter trachea, the lateral tracheal trunk, and the spiracular trachea come together, two smaller tracheae arise (Fig. 5). The larger and more medial of these, the *dorsal trachea* (*DT 3*), corresponds in its position to the dorsal trachea of the mesothorax; it extends dorsally and then medially, and supplies the remotor muscle of the metathoracic coxa, *M. noto-coxalis*. Like the mesothoracic dorsal trachea, it lies just beneath the posterior margin of the postnotum. Just lateral to the base of this metathoracic dorsal trachea arises a finer branch which extends anteriorly into the wing (Fig. 5, *WT 3*). It appears, in some specimens, as an offshoot of the base of the dorsal trachea, and is homologous with the fine mesothoracic trachea which runs from the dorsal trachea to the forewing.

The proximal end of the metathoracic scolopophorous organ attaches to the posterior part of the base of the dorsal trachea, and thus occupies the same position as does the mesothoracic sense organ. At this point it is innervated by a branch of *nervus metathoracicus primus* (Figs. 3, 5, *N 3*). The latter, as has been described in a previous paper (Parsons, '60b), consists of two main branches, one of which extends posteriorly and then laterally, around the promotor muscle of the hindleg, *M. noto-trochantinalis*. In the posteromedial part of the metathorax it sends a

ramus to the tergum; it then passes between the remotor muscle of the leg and a dorsoventral muscle, *Mm. noto-coxalis et dorso-ventralis*, respectively, and sends off a second ramus to the tergum. Laterally it becomes closely associated with the dorsal trachea and follows the latter ventrally to its base, where it innervates the metathoracic scolopophorous organ.

Scolopophorous organs of the first abdominal segment. The first abdominal segment possesses both a discolopodial organ (Fig. 5, *D I*) and a monoscolopodial organ (*M I*). Only the former attaches to a membrane; the latter ends in the connective tissues of the lateral sternal region (Fig. 8). Larsén ('57) has reported a similar situation in both *Corixa* and *Apheloeheirus*, and was the first author to observe the monoscolopodial organ in the Hydrocorisae. In the other aquatic bugs examined by him, only the discolopodial organ appears to be present in the first abdominal segment.

The location of the roughly circular sensory membrane (*SM I*) of the discolopodial organ is shown in Figures 1 and 5. It is almost completely surrounded by the tergal exoskeleton of the reduced first abdominal segment (*I*) (according to Larsén, '57, this sclerite corresponds to the postnota of the thoracic terga). Its anteromedial portion, however, is continuous with the membrane (Fig. 2C, *IS*) between the thoracic and abdominal terga. Larsén ('57) observed a similar connection of the sensory membrane with the intersegmental membrane in the first abdominal segments of all the Hydrocorisae examined by him, with the exception of *Apheloeheirus*. In the latter insect, the sensory membrane is completely surrounded by the exoskeleton.

The sensory membrane is somewhat recessed into the body cavity, and its surface curves inward more than do the membranes of the thoracic organs. The point of attachment of the scolopophorous organ appears as a small, somewhat raised area on the membrane (Fig. 2C). In most specimens this raised area contains one or two tiny dark spots similar to those seen on the metathoracic sensory membrane, and one individual shows a definite, irregularly shaped sclerite here. The sensory membrane of the first abdominal segment is approximately the same size as that of the metathorax and somewhat smaller than that of the mesothorax. Its folds are mostly radially arranged around the point of termination of the discolopodial organ. In the periphery of the membrane a few concentric folds are visible.

From the membrane the discolopodial sense organ runs medially and ventrally, passing just posterior to the first abdominal spiracular trachea (Figs. 3, 5). It attaches to an irregularly shaped sclerite (Fig. 3, *ST*) which lies in the posterior part of the pericoxal membrane of the hindleg (*CM 3*). This sclerite is much more distinct in some individuals than in others. It is movably joined, by a membrane, to the sclerotized abdominal process which surrounds the first abdominal spiracle, and is probably abdominal in nature. On this sclerite originates the more anterior of two dorsoventral muscles (Fig. 5, *MD*) which lie on either side of the second abdominal spiracular trachea (*T II*). The base of the scolopophorous organ, and the nerve which innervates it, run in front of this anterior muscle.

The proximal part of the monoscolopodial organ of the first abdominal segment is joined with that of the discolopodial organ (Figs. 3, 5, 8). Larsén ('57) found a similar close connection of the basal ends of the two organs in *Corixa* and *Aphelocheirus*. The monoscolopodial organ is somewhat finer than the discolopodial organ and is difficult to trace. From its point of attachment on the irregularly shaped ventral sclerite it extends laterally, running parallel and ventral to the discolopodial organ (Fig. 5). Lateral to the first abdominal spiracular trachea it bends ventrally and ends, as in *Corixa* and *Aphelocheirus* (Larsén, '57), in the connective tissue ventral to the sensory membrane of the discolopodial organ (Fig. 8).

Both scolopophorous organs are innervated by a branch of *nervus abdominalis primus* (Figs. 3, 5, 8, *N I*). This branch, which also appears to innervate the muscle of the thoracic gland (Parsons, '60b), runs laterally into the region between the thorax and the abdomen and then extends ventrally into the area immediately anterior to the caudal part of the metathoracic pericoxal membrane. Here it runs anterior to the irregularly shaped sclerite of the latter membrane, and joins the combined bases of the two scolopophorous organs.

Scolopophorous organ of the second abdominal segment. The discolopodial organ of the second abdominal segment of *Gelastocoris* differs in several ways from the other discolopodial organs. Unlike the latter, it ends on unmodified exoskeleton rather than on a membrane. Its distal end, which appears to be somewhat broader than the rest of the organ, terminates in the hypodermis of the sternum of the second abdominal segment, medial to the region where the latter overlies the metathoracic coxa, and near the posterior border of the segment (Figs. 3, 5). From this point

of attachment the organ (*D II*) extends anterolaterally and somewhat dorsally; in this respect it also differs from the more anterior scolopophorous organs, which extend medially from their distal attachments rather than laterally. It is very difficult to trace the course of the second abdominal scolopophorous organ, both in dissections and in histological preparations, since it runs through a large mass of connective tissue.

Unlike the other scolopophorous organs, that of the second abdominal segment is not necessarily attached proximally to any other structure. In some specimens its base was associated with a fine tracheal branch from the second abdominal spiracle; in many others, however, it lay free in the body cavity. None of the individuals examined showed any connection between the proximal end of the organ and the integument of the body wall.

The scolopophorous organ is innervated by a branch of *nervus abdominalis secundus* (Figs. 3, 5, *N II*) in the lateral part of the body cavity, lateral to the second abdominal spiracle. This nerve passes ventrally between the second abdominal spiracular trachea and the more posterior of the two dorsoventral muscles which lie near that trachea. The nerve and the scolopophorous organ of this segment, unlike those of the preceding segments, form a sharp angle with each other. Also, unlike the nerves to the more anterior sense organs, the nerve supplying the organ of the second abdominal segment does not end at the base of the organ but branches and continues laterally into the side of the abdomen.

A scolopophorous organ has been described in the second abdominal segment of only one other heteropteran. Larsén ('55; '57) has reported a monoscolopodial organ, in the second abdominal segment of *Aphelocheirus,* which, like the discolopodial organ of *Gelastocoris*, attaches distally to the ventral body wall. It differs from the scolopophorous organ of *Gelastocoris*, however, in two major respects: it consists of one rather than two sensilla, and its basal end is always associated with a tracheal sac, of a peculiar structure, which lies close to the second abdominal spiracle in *Aphelocheirus.*

Histological Observations

In *Gelastocoris,* each *scolopophorous organ* or *scoloparium* consists of either one or two *sensilla* or *scolopodia.* In the discolopodial organs the two sensilla lie side by side, and the boundary between them is rarely distinguishable. The sensilla of all five scolopophorous organs show the same basic histological structure.

Histological preparations reveal that the gelastocorid sensilla are composed of three types of cells (Fig. 6): a distal *cap cell* (*CC*) (Snodgrass, '35; "Deckzelle" of German authors; possibly the "attachment cell" of Gray, '60), an intermediate *enveloping cell* (*EC*) (Snodgrass, '35; "Hüllzelle" of German authors),

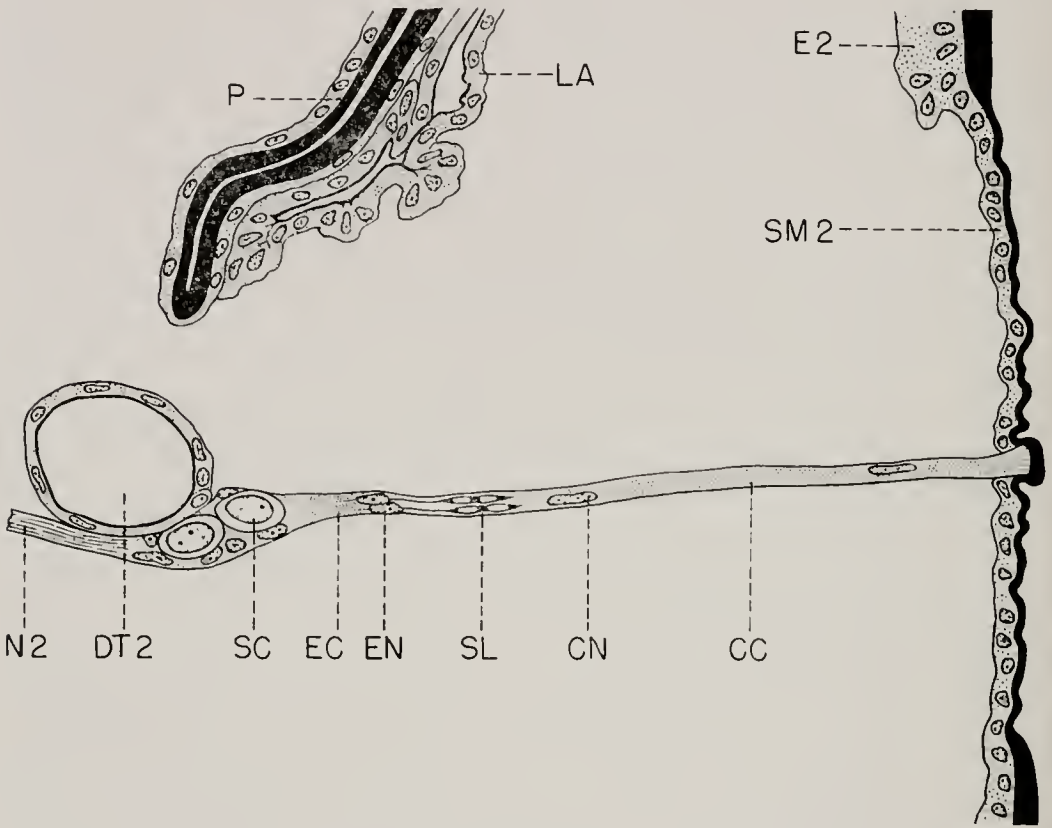

Fig. 6. Frontal section through the right side of the mesothorax, showing the mesothoracic discolopodial organ and its relation to the dorsal trachea and sensory membrane (reconstructed from several consecutive serial sections). Sclerotized structures are shown in solid black. Lateral region is at the right, medial region at the left. X425.

and a proximal, basal *sensory cell* (*SC*) (Snodgrass, '35; "Sinneszelle" of German authors). Between the enveloping cell and the cap cell lies a spindle-shaped sensory rod or *scolops* (*SL*) (Snodgrass, '35; "Stift" of German authors; "scolopale" of Gray, '60). The appearance and position of these elements in the sensillum corresponds, in general, to the descriptions of previous authors (Eggers, '28; Wotzel, '33; Larsén, '57) who examined other Heteroptera by means of the light microscope.

In the discolopodial organs of the mesothorax, metathorax, and first abdominal segment, the two cap cells of the paired sensilla attach to sensory membranes. In a few preparations the endings

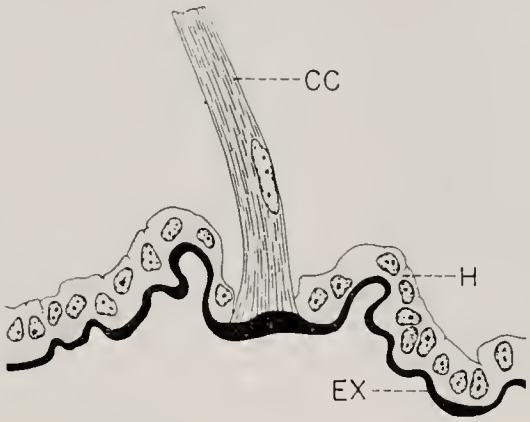

Fig. 7. Detail of the point of attachment of the first abdominal discolopodial organ on its sensory membrane. Frontal section. X400.

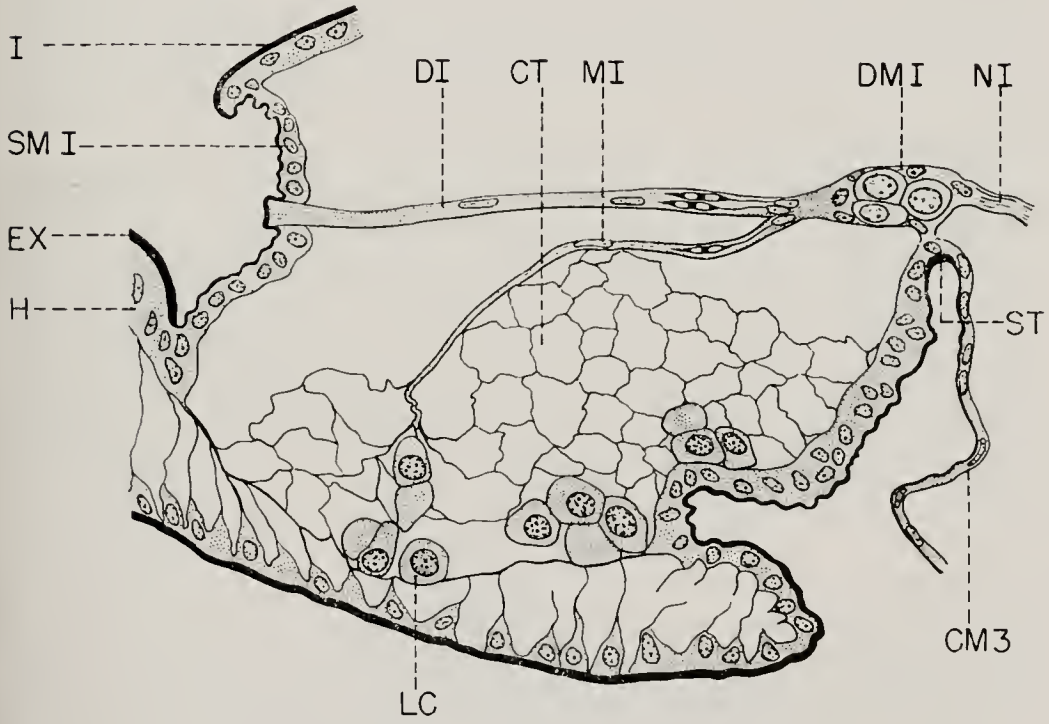

Fig. 8. Cross section through the lateral part of the first abdominal segment, in the region of the discolopodial and monoscolopodial organs (reconstructed from several consecutive serial sections). Lateral region is shown at the left, medial region at the right, dorsal region at the top, ventral region at the bottom. X225.

of the two sensilla upon the membrane are distinct from one another; in most sections, however, the sensilla lie so closely together that only a single ending of the scolopophorous organ is evident (Fig. 7). There appears to be little, if any, increase in the number of hypodermal cells around the area of attachment. Although the point of attachment is not greatly differentiated, the cuticula of the membrane in this region usually appears somewhat thicker and more lightly stained than the surrounding cuticula, and is slightly raised above the level of the surrounding membranous folds.

The cap cell of the first abdominal monoscolopodial organ appears to branch into many fine processes in the ventral part of the abdominal body cavity, just beneath the membrane of the first abdominal discolopodial organ (Fig. 8). In this area, and throughout the abdomen, lie many large cells (*LC*) with deeply staining nuclei containing large chromatin granules. Their granular cytoplasm stains gray in Mallory's triple connective tissue stain and sometimes contains small vacuoles. These cells, which are spherical or oval in form, usually occur in clumps. The fine branches of the cap cell of the monoscolopodial organ seem to be continuous with the connective tissue (*CT*) in this region and to be closely associated with these clumps of large cells; they appear to end eventually in the hypodermis of the ventral body wall.

The discolopodial organ of the second abdominal segment also terminates in the hypodermis of the body wall. Unlike the more anterior discolopodial organs, however, it is not associated with a membrane and the exoskeleton overlying the point of attachment is not modified in any way. The two sensilla could be traced to their point of termination in approximately half of the sense organs examined histologically; one preparation (Fig. 9) shows a clear two-part separation of the sensilla in this region.

Fig. 9. Detail of the point of attachment of the second abdominal discolopodial organ in the hypodermis of the second abdominal sternite. X1000.

In the sensilla of all five organs, the very elongate cap cells possess a fibrillar, lightly-staining cytoplasm and elongate nuclei (*CN*) which contain few chromatin granules of various sizes (Fig. 10). According to Eggers ('28), both the cap cell and the enveloping cell represent modified supporting cells. The position of the nucleus of the cap cell in *Gelastocoris* is extremely variable; this variation is evident not only among different individuals but between the scolopophorous organs of the two sides of one specimen, or between the two sensilla of a single scolopophorous organ. The nucleus may lie anywhere within the cell; it is, however, more commonly present in the proximal half than in the distal half of the latter. Larsén ('57) has pointed out this variation in the position of the nucleus in the cap cells of *Aphelocheirus*.

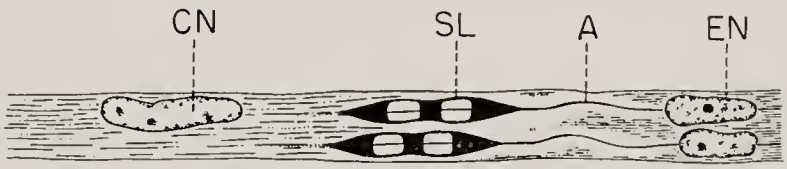

Fig. 10. Detail of part of the right mesothoracic discolopodial organ. Frontal section through the body, taken in the region of the scolops.

Proximal to the cap cells lie the elongate but shorter enveloping cells (Figs. 6, 10). Although Larsén ('57) reported a more alveolar, lighter-staining cytoplasm in the latter than in the former, the fibrillar cytoplasm of the enveloping cells stains considerably darker than that of the cap cells in *Gelastocoris*. The boundary between the cap and enveloping cells is not clear in any of the preparations; it lies somewhere at the level of the scolops. The elongate nucleus of the enveloping cell (*EN*) is located just proximal to the scolops. In the discolopodial organs the nuclei of the two enveloping cells lie at approximately the same level.

The scolops is a spindle-shaped body staining a deep red in Mallory's triple connective tissue stain. Its form is similar to that described in many Hydrocorisae by previous authors (Fig. 10). Cross sections through the scolops reveal that it is hollow, with a slender process running through its center from the proximal to the distal end. The two ends and the medial, somewhat indented central portion of the scolops are encircled by thickened rings. Between these rings the walls of the scolops

are thinner and appear to be composed of five or six ribs which run parallel to the longitudinal axis of the scolops. This appearance of the scolops is in general agreement with the previous descriptions of Hagemann ('10; *Corixa*), Wefelscheid ('12; *Plea*), and Eggers ('28; *Plea* and Corixidae).

The proximal part of the scolops is surrounded, in most preparations, by a vacuolar space (Fig. 10) which is probably an artifact (Gray, '60). In the discolopodial organs, the scolopes of the two sensilla lie either side by side or one slightly distal to the other. The scolops of the monoscolopodial organ in the first abdominal segment is located just ventral to the scolopes of the discolopodial organ of that segment. The slender central process of the scolops continues proximally through the vacuolar space and the region of the enveloping cell, and appears to extend into the sensory cell area. This proximal strand (Fig. 10, *A*) represents the "Achsenfaden" of previous authors.

Gray's ('60) recent electron microscope study of the abdominal tympanal organ of *Locusta* has revealed much concerning the fine structure of the scolops. The latter, which he termed the "scolopale," is an intracellular, fibrous structure within a "scolopale cell." The "scolopale cell" may correspond to the enveloping cells of the present study, but this is uncertain; the electron microscope reveals more cells in the sensillum than does the light microscope, and their appearance is considerably different in *Locusta* and *Gelastocoris*. Gray confirmed the observation, made in the present study, that the walls of the scolops are composed of thickened rods; he further observed that these rods may branch. Fitting over the distal end of the "scolopale cell" is an extracellular, fibrous "scolopale cap." This cap, along with the merged distal ends of the "scolopale rods," probably corresponds to the distal thickened ring observed in the scolops of *Gelastocoris*, while the fusion of the proximal ends of the rods produces the most proximal ring. The electron microscope shows that the dendrite of the sensory cell ends within the base of the scolops, and from its point of termination a cilium projects distally into the "scolopale cap." This cilium probably corresponds to the slender central process observed in the scolops of *Gelastocoris*. Gray described a system of branching rootlets at the base of the cilium. These rootlets extend proximally, within the dendrite, nearly to the nucleus of the sensory cell; they probably represent the "Achsenfaden" of the present study.

In some preparations of *Gelastocoris* a distal process from the scolops could be observed running for a short distance through the region of the cap cells. Whether this process (the "Endfäden" of previons authors) extends to the distal end of the cap cells could not be determined; if so, it is much finer and more difficult to see distally than proximally. Eggers ('28) considered the scolopophorous organs of the Hydrocorisae to be "amphinematic," a term used for organs whose "Endfäden" extend all the way to the integument. Wotzel ('33), however, reported that the Hydrocorisae lack "Endfäden" and thus possess "mononematic" scolopophorous organs. Larsén ('57), although unable to trace the "Endfäden" to the end of the cap cells in most of his preparations of Hydrocorisae, believed them to be present in all. Gray's ('60) study, unfortunately, offers no hints as to the nature of the "Endfäden."

At the base of the sensillum lies a large sensory cell (Figs. 6, 11, *SC*) with granular, lightly-staining cytoplasm and a round nucleus containing few chromatin granules. In the discolopodial organs the sensory cells of the two sensilla lie close together and are surrounded by *supporting cells* (Fig. 11, *SUP*) ("akzessorische Zellen" or "Hüllzellen" of previous authors). The

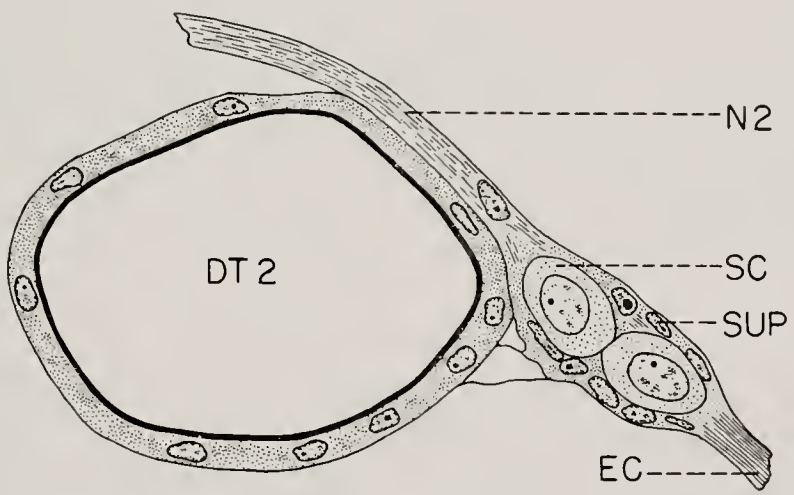

Fig. 11. Detail of the base of the left mesothoracic discolopodial organ. Frontal section through the body. Anterior region is shown at the bottom, posterior region at the top. X975.

latter, which form a sort of capsule ("Hüllschicht" of Wotzel, '33) around the two sensory cells, are variable in size. They are smaller than the sensory cells and their nuclei are richer in

chromatin. Both the sensory and the supporting cells are enclosed by a membrane which is continuous with the neurilemma of the nerve innervating the scolopophorous organ. The bases of the mesothoracic and metathoracic scolopophorous organs, which lie beside tracheae, are connected to the latter by fine processes from the supporting cells (Fig. 11), and the combined bases of the monoscolopodial and discolopodial organs in the first abdominal segment (Fig. 8, *DM 1*) are similarly attached to the sternum.

In two of the seven sectioned specimens, a fine nerve (Fig. 12, *N*) was observed coming off from the area of the sensory cells at the base of the metathoracic scolopophorous organ. This was clearly seen on both sides of one individual; in the second, which

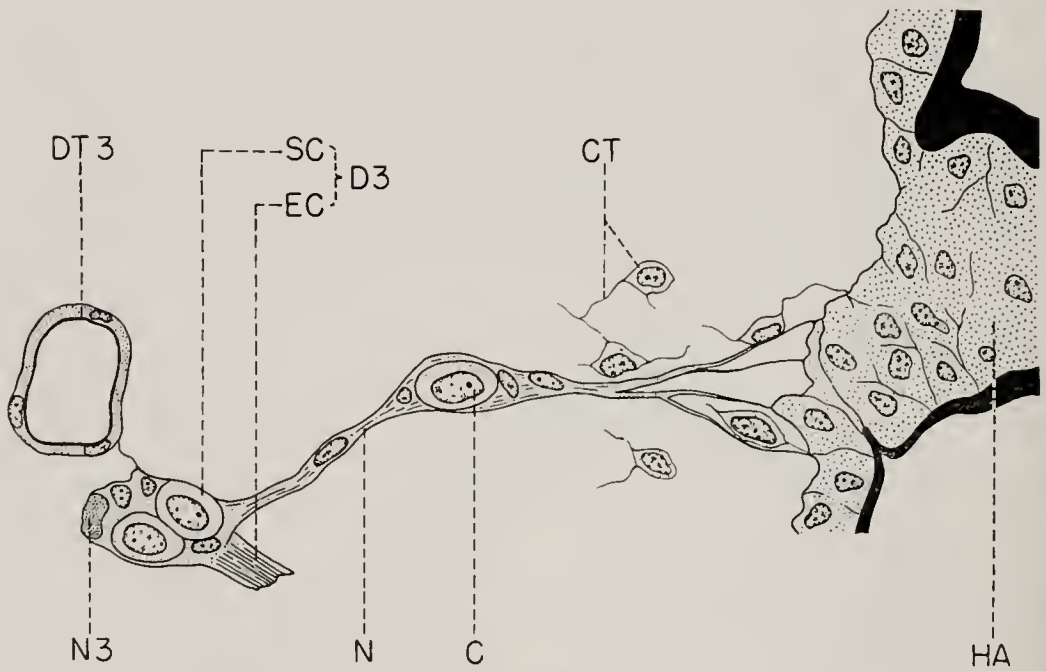

Fig. 12. Detail of the base of the left metathoracic discolopodial organ, showing the slender nerve which arises from this region. Cross section through the body, taken posterior to the point at which the discolopodial organ attaches to its sensory membrane. Dorsal region is shown at the right, ventral region at the left, medial region at the top, lateral region at the bottom. X700.

was poorly preserved, it appears to be present on at least one side. The nerve, which is much more slender than the scolopophorous organ, leads to a large cell (*C*) which resembles, in its size and staining properties, the sensory cells of the sensilla.

Grouped around this cell are several smaller cells resembling the supporting cells at the base of the scolopophorous organ. Distal to the large cell the nerve sends slender branches through the connective tissues to the hypodermis in the region of the axillary cord (*HA*), posterior to the point of termination of the scolopophorous organ on its membrane. Wotzel ('33) observed a fibrous "Strang," associated with the metathoracic scolopophorous organs of *Naucoris,* which resembles this nerve in *Gelastocoris* and which contains a similar large and apparently sensory cell. In *Naucoris* the "Strang" appears to be considerably longer than the nerve of *Gelastocoris* and to run closer and more parallel to the scolopophorous organ. According to Wotzel, the processes at the distal end of the "Strang," which run to the hypodermis, end very close to the point of attachment of the scolopophorous organ. In *Gelastocoris,* the fine processes distal to the large cell appear to meet the integument at a point more distant from the termination of the scolopophorous organ.

In the first abdominal segment, the sensory cell of the monoscolopodial organ lies beside the two sensory cells of the discolopodial organ (Fig. 8). All three cells appear to be surrounded by a common layer of supporting cells and innervated by the same nerve. In many preparations a broad ligament was observed connecting the bases of the two scolopophorous organs with the irregularly shaped selerite of the posterior pericoxal membrane, which has been previously described. The monoscolopodial organ separates from the discolopodial organ at approximately the level of the nuclei of the enveloping cells.

The base of the discolopodial sense organ of the second abdominal segment, unlike that of the first segment, is not connected with the integument but lies free in the lateral part of the body cavity. In approximately half of the preparations in which the base of the organ could be observed clearly, it was not associated with any other structure in the body cavity; in the rest, it lay close beside a fine trachea from the second abdominal spiracle. Two of the latter specimens showed some attachment of the sensory cell area to the trachea by means of processes from the supporting cells; in the other preparations the basal part of the scolopophorous organ lay beside the trachea but was not attached to it. The occurrence of an attachment with a trachea appears to be quite variable; the two specimens in which a connection was observed showed this condition only on one side of the body.

DISCUSSION

Previous studies on the anatomy of the head (Parsons, '59), the thorax (Parsons, '60a), and the nervous system (Parsons, '60b) of *Gelastocoris* have revealed a marked morphological similarity between this insect and the aquatic bugs or Hydrocorisae. These similarities support the theory of China ('55) and earlier workers that the Gelastocoridae and the aquatic Heteroptera are closely related phylogenetically. The presence of scolopophorous organs in *Gelastocoris* may provide additional morphological evidence in favor of this theory. Larsén ('57) has reported that similar organs have not yet been described in either the terrestrial bugs (Geocorisae) or the semi-aquatic forms (Amphibicorisae), and he was unable to find them in representatives of those two groups (further research may, of course, reveal their presence in the latter). The terrestrial and semi-aquatic bugs also lack mesothoracic air sacs, and in them the subalar air space is either absent or poorly developed (Larsén, '57); in *Gelastocoris* the air space is well developed, and air sacs, although not inflated, are present.

The scolopophorous organs of *Gelastocoris* are, in general, very similar to those of the aquatic bugs. The position and appearance of the sensory membranes of the three anterior discolopodial organs, and their location within the subalar air space, are the same in *Gelastocoris* as in the Hydrocorisae. The basal attachment of the pterothoracic organs upon tracheae, which has been noted in *Gelastocoris,* is also found in most aquatic bugs (Larsén, '57); similarly, in both groups the scolopophorous organs of the first abdominal segment attach proximally upon the sternum. Histologically, the sensilla of *Gelastocoris* are nearly identical with those of the Hydrocorisae as described by other authors. The monoscolopodial organ of the first abdominal segment of *Gelastocoris,* which has been previously reported in only two aquatic Heteroptera, *Corixa* and *Aphelocheirus,* is similar in all three of these insects.

In two respects the scolopophorous organs of *Gelastocoris* differ from those of the aquatic bugs. First, the arrangements of the tracheal system in the mesothorax is unlike that of any of the Hydrocorisae thus far described. On the basis of the tracheal system and its relationship to the mesothoracic scolopophorous organ, Larsén ('57) grouped the Hydrocorisae into three main categories. In *Nepa, Ranatra, Belostoma, Naucoris,* and *Notonecta,* two air sacs are present, a "vordere" and a "hintere Tracheenblase"; the former lies close to the membrane of the

scolopophorous organ, although it is not intimately associated with it. The lateral air sac of *Gelastocoris,* which is probably homologous with this "vordere Tracheenblase," does not lie anywhere near the membrane. Also, the probable homologue of the "hintere Tracheenblase," the dorsal trachea of *Gelastocoris,* is not developed into an air sac. In *Aphelocheirus,* which falls into Larsén's second category, air sacs are absent in the adults of at least one species (*A. aestivalis*) although they are present in the nymphs. *Gelastocoris,* on the other hand, shows air sacs in the adults but not in the nymphs. In *Corixa,* which forms Larsén's third category, an air sac corresponding to the "hintere Tracheenblase" of the other Hydrocorisae is intimately associated with the sensory membrane of the mesothoracic scolopophorous organ. No such intimate association of an air sac with the membrane was observed in *Gelastocoris.*

A second difference from the Hydrocorisae is the occurrence, in *Gelastocoris,* of discolopodial organs in the second abdominal segment. Only *Aphelocheirus* possesses scolopophorous organs in that segment, and in that insect, as has been previously noted, the organs are monoscolopodial and, unlike those of *Gelastocoris,* associated with a tracheal sac.

The function of the scolopophorous organs in the Hydrocorisae is, as yet, not definitely established. Larsén ('57) has presented a thorough and critical discussion of this problem, and the reader is referred to his paper for an extensive review of the literature on the subject. Most previous workers have considered the scolopophorous organs of the aquatic bugs to be tympanal hearing organs. This view is supported by the fact that in such groups as the Orthoptera, Lepidoptera, and Homoptera, sense organs resembling the pterothoracic and first abdominal discolopodial organs of the Heteroptera and, like them, attaching to membranes, are almost certainly sound perceptive. Also, many aquatic bugs such as the Corixidae, *Naucoris, Plea,* and *Ranatra* are known to stridulate (Larsén, '57).

Hagemann's ('10) experiments upon *Corixa* led him to conclude, with some reservations, that the corixid mesothoracic scolopophorous organ could perceive sound. Wefelscheid ('12; *Corixa* and *Plea*) and Schaller ('51; *Corixa*) also considered the mesothoracic organ to be a tympanal organ, and Wotzel ('33) believed the morphology of the scolopophorous organs in the Hydrocorisae to indicate that they are sound-perceiving structures. Eggers ('28), however, was uncertain as to whether they could be considered true tympanal organs.

Larsén ('57) has criticized the theory that the three anterior pairs of discolopodial organs in the Hydrocorisae are tympanal (he did not discuss the possible function of those scolopophorous organs which are not attached to membranes). He noted that an increase in the internal body pressure of a water bug causes the scolopophorous sensory membranes to bulge outwards, whereas other membranes, such as the subalar one, are unaffected by internal pressure changes. Such a reaction, he felt, indicates that the sensory membranes are not tympanal. He also pointed out that the membranes of the tympanal organs in other insects are tightly stretched, whereas those of the scolopophorous organs in the Hydrocorisae (with the exception of the corixid mesothoracic organ) are not tightly stretched but folded. Only in the mesothorax of the Corixidae, he believed, is there reason to presume that the scolopophorous organ has a sound perceptive function. The highly complex structure of the membrane of the corixid mesothoracic organ, which differs considerably from that of other Hydrocorisae, has been described by many authors (Hagemann, '10; Wefelscheid, '12; Eggers, '28; Wotzel, '33; Schaller, '51; Larsén, '57).

Larsén ('57) has proposed another possible function for the scolopophorous organs of the Hydrocorisae, that of orientation perception. He cited the facts that the sensory membranes of the three anterior pairs of organs all face externally onto a common subalar air space, and that they bulge outwards in response to an increased pressure from the internal body fluid. He further pointed out that the sensory membranes are bilaterally paired and arranged antero-posteriorly along the body. Larsén proposed that the pressure of the body fluid upon each of the membranes would vary according to the orientation of the body. He reasoned that those membranes lying at a lower level with respect to gravity would be subjected to more pressure from the internal body fluid than those higher up, and would, consequently, bulge further outwards, producing a greater tension upon the scolopophorous organs.

The discovery of scolopophorous organs in *Gelastocoris* does not shed much light upon the problem of their function. No experiments have been carried out to determine whether or not this insect is sensitive to sound. Stridulation has never been reported in *Gelastocoris*, and the author has never observed it in animals kept under laboratory conditions. However, stridulation has also not been demonstrated in some of the aquatic bugs possessing scolopophorous organs. Larsén's proposal that these

organs may detect changes in the body's orientation appears, to the present author, to be somewhat questionable. Obviously, the problem of the function of the scolopophorous organs in *Gelastocoris,* as in the Hydrocorisae, cannot be resolved on the basis of morphology alone but requires, as Larsén ('57) has pointed out, further experimental work.

SUMMARY

Paired scolopophorous organs, similar to those described by other authors in the aquatic Heteroptera (Hydrocorisae), are present in the mesothorax, the metathorax, and the first two abdominal segments of the shore-dwelling heteropteran *Gelastocoris oculatus* (Fabricius). The pterothoracic and first abdominal segments contain discolopodial organs, each composed of two sensory sensilla, which attach to membranes located on the body wall within the subalar air space. The first abdominal segment also possesses a pair of monoscolopodial organs, terminating in the connective tissue in the ventral part of the abdomen, each of which consists of a single sensillum. The gross and histological morphology of these organs is similar to that of the scolopophorous organs of the Hydrocorisae, as described by previous authors. In addition, *Gelastocoris* possesses, in the second abdominal segment, a discolopodial organ which terminates on the sternum and is not associated with a membrane. Such an organ has not yet been reported in the Heteroptera. It differs from the second abdominal scolopophorous organ of *Aphelocheirus* since it contains two rather than one sensilla and is not necessarily associated with the tracheal system.

The presence of these organs in *Gelastocoris* supports the theory of China ('55) and other authors that the Gelastocoridae are closely related to the Hydrocorisae. Comparable organs appear to be absent in the semi-aquatic and terrestrial bugs.

The function of the scolopophorous organs of *Gelastocoris* is unclear. They may be involved with hearing or with orientation perception; previous authors have proposed these as two possible functions for the scolopophorous organs of the Hydrocorisae.

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I am indebted to Mr. Edwin P. Marks, of Washburn University, and to the members of the C. V. Riley Entomological Society, of Columbia, Missouri, who provided the insects used in this investigation. I am also grateful to my husband, Dr. Thomas S.

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EXPLANATION OF FIGURES

In the figures, the number "2" after an abbreviation indicates a mesothoracic structure, while a "3" indicates a metathoracic structure. The numerals "I" and "II" indicate structures of the first and second abdominal segments respectively.

The abbreviations used are as follows:

A – proximal strand of scolops ("Achsenfaden")
B – postalar bridge
C – large cell in nerve from base of metathoracic scolopophorous organ
CC – cap cell
CM – pericoxal membrane
CN – nucleus of cap cell
CT – connective tissue
CX – coxal cavity
D – discolopodial organ
DM I – combined bases of discolopodial and monoscolopodial organs of the first abdominal segment
DT – dorsal trachea
E – epimeron
EC – enveloping cell
EN – nucleus of enveloping cell
ES – episternum
EX – exoskeleton
F – furca
FW – forewing
H – hypodermis
HA – hypodermis in region of metathoracic axillary cord
HW – hindwing
IS – intersegmental membrane between thorax and abdomen
L – lateral tracheal trunk
LA – lateral air sac
LC – large cells in abdominal connective tissue
M – monoscolopodial organ
MA – medial air sac
MD – dorsoventral muscles of second abdominal segment
MS – *M. coxa-subalaris*
N – nerve
N 2 – *nervus mesothoracicus primus*
N 3 – *nervus metathoracicus primus*
N I – *nervus abdominalis primus*
N II – *nervus abdominalis secundus*
NM – notum
P – pleural apophysis
PE – prealar membrane
PM – parapsidal membrane
PN – postnotum
R – pleural ridge
S – subalare
SB – subalar membrane
SC – sensory cell
SL – scolops
SM – sensory membrane of discolopodial organ
SP – metathoracic spiracle
ST – irregular sclerite in metathoracic pericoxal membrane
SUP – nucleus of supporting cell
T – spiracular trachea
TN – trochantin
WT – trachea to wing
I – first abdominal segment
II – second abdominal segment

LITERATURE CITED

Brocher, F.

1909. Recherches sur la respiration des insectes aquatiques adultes. La notonecte. Ann. Biol. Lacustre, **4**: 9-32.

China, W. E.

1955. The evolution of the water bugs. Bull. Nat. Inst. Sci. India, **7**: 91-103.

Eggers, F.

1928. Die stiftführenden Sinnesorgane. Morphologie und Physiologie der chordotonalen und der tympanalen Sinnesapparate der Insekten. Zool. Bausteine, **2**: 1-354.

Gray, E. G.

1960. The fine structure of the insect ear. Phil. Trans. Roy. Soc. London, (B), **243**: (700): 75-94.

Hagemann, J.

1910. Beiträge zur Kenntnis von *Corixa*. Zool. Jahrb. (Abt. Anat.), **30**: 373-426.

Hamilton, M. A.

1931. The morphology of the water-scorpion, *Nepa cinerea* Linn. (Rhynchota, Heteroptera). Proc. Zool. Soc. London, 1931: 1067-1136.

Larsén, O.

1955. Spezifische Mechanorezeptoren bei *Aphelocheirus aestivalis* Fabr. nebst Bemerkungen über die Respiration dieser Wanze. Lunds Univ. Årsskrift., N.F., (2) **51** (11): 1-59.

1957. Truncale Scolopalorgane in den pterothorakalen und den beiden ersten abdominalen Segmenten der aquatilen Heteropteren, *Ibid.*, N.F., (2) **53** (1): 1-68.

Maulik, S.

1916. The respiratory system of *Nepa cinerea*, Linn. J. Zool. Res., **1**: 41-58.

Parsons, M. C.

1959. Skeleton and musculature of the head of *Gelastocoris oculatus* (Fabricius) (Hemiptera-Heteroptera). Bull. Mus. Comp. Zool. Harv. Coll., **122**: 1-53.

1960a. Skeleton and musculature of the thorax of *Gelastocoris oculatus* (Fabricius) (Hemiptera-Heteroptera). *Ibid.*, **122**: 299-357.

1960b. The nervous system of *Gelastocoris oculatus* (Fabricius) (Hemiptera-Heteroptera). *Ibid.*, **123**: 131-199.

Presswalla, M. J. and G. J. George

1935. The respiratory system and the mode of respiration of the water-bug *Sphaerodema rusticum* Fabr., with remarks on those of *Nepa, Laccotrephes,* and *Ranatra*. Proc. Ind. Acad. Sci., (B), **2**: 280-315.

SCHALLER, F.

1951. Lauterzeugung und Hörvermögen von *Corixa* (*Callicorixa*) *striata* L. Zeitschr. vergl. Physiol., **33**: 476-486.

SNODGRASS, R. E.

1935. Principles of insect morphology. McGraw-Hill, New York and London.

WEFELSCHEID, H.

1912. Uber die Biologie und Anatomie von *Plea minutissima* Leach. Zool. Jahrb. (Abt. Syst.), **32**: 389-474.

WOTZEL, F.

1933. Zur Kenntnis der Tympanalorgane der Hydrocores. Zeitschr. wiss. Zool., **143**: 241-262.

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THE MAMMALIAN FAUNA OF THE DIVISADERO LARGO FORMATION, MENDOZA, ARGENTINA

BY GEORGE GAYLORD SIMPSON,
JOSÉ LUIS MINOPRIO, AND
BRYAN PATTERSON

WITH SEVEN PLATES

CAMBRIDGE, MASS., U.S.A.
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No. 4 — *The Mammalian Fauna of the Divisadero Largo Formation, Mendoza, Argentina*

By George Gaylord Simpson,[1]
José Luis Minoprio,[2] and
Bryan Patterson [1]

INTRODUCTION

The presence of thick series of sedimentary rocks in the Andine precordillera of Mendoza has been known since the earliest days of geological exploration. In a general way, it was noted by Darwin, who visited the area in 1835 and published on its geology in 1846. It was early recognized that some of these sediments are Triassic, and studies concentrating on that part of the sequence have been numerous (see Minoprio, 1958, also review and extensive references in Romer, 1960). Demonstration that part of the post-Triassic sequence belongs somewhere in the Eogene was, however, comparatively tardy. The first definite proof of that fact was probably the discovery of a hegetothere (named *Ethegotherium* on a later page of this paper) in the region of Cerro Divisadero Largo some eight kilometers west of the city of Mendoza. In June, 1936, while on a botanical excursion, Adrián Ruiz Leal found a rock fragment that contained that specimen and took it to his home, where it remained until Minoprio became cognizant of it and asked Ruiz Leal for the fossil and for permission to study the occurrence (Minoprio, 1947).

From 1943 to 1946 Olivo Chiotti made a geological map and stratigraphic study of the region. His thesis has not been published, but the manuscript has been available to those interested and data from it have been included in several publications (especially Minoprio, 1947; Simpson and Minoprio, 1949). First recognition and definition of a Divisadero Largo formation were based on Chiotti's work. Chiotti found further vertebrate fossils, which were sent to the Museo de La Plata and tentatively identified, but not published upon, by Ángel Cabrera, who recognized their early Tertiary character and considered them possibly Eocene. Minoprio began his study of and collecting in the Divisadero Largo in connection with his identification of the first find

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and with Chiotti's field project. In 1946 Minoprio showed the fossil localities to Carlos Rusconi, who with M. Tellechea made further collections from the Divisadero Largo formation.

The first publications on the fauna were made independently and based on different collections by Minoprio (1947) and by Rusconi (1946a, b, c). Other specimens found by Minoprio have been described by Simpson and Minoprio (1949, 1950 [1]), and in extension of that work Minoprio (1951) published a preliminary stratigraphic note. Since then Minoprio has continued to collect in the Divisadero Largo as opportunity presented, and he discovered the important extension of the fossil-bearing beds to Papagallos, all earlier collections being from the type locality only. A number of other paleontologists and geologists, both Argentine and foreign, have visited the area through the years and most of them have picked up some specimens, but further publication has been only that by Patterson (1952) on one of the specimens found by Federico García Romeu and Osvaldo A. Reig in 1951. Patterson and Simpson visited the Divisadero Largo under Minoprio's guidance in 1952 and 1955 respectively, and in 1958 a joint expedition of the Museum of Comparative Zoology (Harvard University) and the Museo Argentino de Ciencias Naturales (Buenos Aires), including A. S. Romer and Patterson, made a collection there.

For the past ten years the present three authors have been accumulating further materials and observations with the hope of producing a more nearly definitive study of this important and peculiar fauna. Publication has been repeatedly deferred as new specimens required emendation or new problems called for better evidence. It is still quite impossible to produce anything like a definitive study or to solve all major problems, but we have decided that a halt must be called at this point and that what is now available should be published. We have been able to study most, although not quite all, of the mammalian fossils known to have been collected from the Divisadero Largo. So many people have picked up odd specimens that there are doubtless some of whose existence we are unaware. The most extensive collections by Minoprio have been studied not only by him but also, at first hand, by Simpson, and most of them also by Patterson. Other collections in Mendoza, Buenos Aires, and La Plata have been

1 This is an abbreviated Spanish version of Simpson and Minoprio (1949). Through an editorial oversight, a genus and two species were said to be new in the Spanish version. They were in fact new in the English version published in the previous year.

studied especially by Patterson, among the present authors. Materials in New York and Cambridge have been studied by Simpson and Patterson. In this connection we are much indebted to the Museo de La Plata and Dr. Rosendo Pascual, the Museo Argentino de Ciencias Naturales and Dr. Noemí Cattoi, and the Museo de Historia Natural de Mendoza and Sr. Carlos Rusconi. The late Dr. Ángel Cabrera kindly provided Minoprio with extensive notes on the Chiotti collection in the Museo de La Plata, and his courtesy is gratefully recorded even though our treatment of that collection is based on first-hand study mainly by Patterson.

Some of the work included in this paper was done by Simpson while on the staff of the American Museum of Natural History and some manuscript drafted there was released for publication here. Copy for the new Figures 5-6 and 8-9 (drawn by John Le Grand) and for Plates 1-4 was provided by that museum, and the original copy for Figures 2-3, 16, and 21 and Plate 6 (photograph), previously published in Simpson and Minoprio (1949), was also furnished for reproduction here. We are glad to acknowledge this cooperation from what is now the Department of Vertebrate Paleontology of that institution and from Dr. E. H. Colbert, its present chairman.

Figures 4, 7, 10-15, 17, and 19-20 and Plate 6 (section) are new and have been drawn for the Museum of Comparative Zoology by Mrs. Dorothy H. Marsh, in some instances from sketches by Patterson, as indicated in the captions, and in others from the specimens. It is to be understood that Patterson's sketches were necessarily made rather rapidly and free-handedly. They are believed to represent structures adequately, but may not be exactly in scale as to details.

Simpson's visit to Mendoza in 1955 was a side trip made possible by his presence in southern Brazil under the auspices of the Conselho Nacional de Pesquisas of the United States of Brazil.

Patterson's studies of Divisadero Largo specimens in Argentina and his visit to the locality during 1952 were carried out during tenure of a John Simon Guggenheim Memorial Foundation Fellowship. The joint Museum of Comparative Zoology-Museo Argentino de Ciencias Naturales expedition was supported in part by grants from *Life* magazine and the National Science Foundation. To these organizations we express our sincere thanks.

In order to expedite this publication, we have confined it to the mammals. Rusconi (1946b, c) has described a bird, *Cunampaia simplex,* and a crocodilian, *Ilchunia parca,* from the Divisadero Largo, and Minoprio (1947) figured but did not name or identify a turtle carapace. Considerably more unpublished material of chelonians, crocodilians, and snakes is known to us. Some of those specimens are of great interest, but they evidently will not add significantly to the evidence of the mammals on the main problems presented by the fauna. Adequate treatment of the nonmammals will require considerable further study, preferably by specialists in the respective groups. At present we remark only that the bird *Cunampaia,* although its relationships have not been determined, definitely does not belong to the "Stereornithes" (Phororhacoidea), to which it was originally referred by Rusconi (see Patterson and Kraglievich, 1960).

The following designations are used for the various collections:

A.M.N.H. American Museum of Natural History, New York. In general these catalogue numbers are those of casts, not the originals, of specimens collected by Minoprio and now deposited in Argentine museums, but they thus precisely designate the originals.

M.A.C.N. Museo Argentino de Ciencias Naturales, Buenos Aires. These include the first discovery made by Ruiz Leal, other specimens collected by Minoprio, and still others by the joint M.C.Z.–M.A.C.N. expedition.

M.C.Z. Museum of Comparative Zoology at Harvard College, Cambridge. Collected by Patterson and others on the joint M.C.Z.–M.A.C.N. expedition.

M.H.N.M. Museo de Historia Natural de Mendoza, Mendoza. Specimens collected by Rusconi and Tellechea and by Minoprio.

M.L.P. Museo de La Plata, La Plata. Specimens collected by Chiotti and by Castro.

M.M.M.P. Museo Municipal de Ciencias Naturales y Tradicionales de Mar del Plata, Mar del Plata. Reference is to a single specimen (*Groeberia*), of which a description has already been published, collected by García Romeu and Reig. Other specimens in that collection were kindly made available to us for a time, but they apparently represent no species not otherwise known and it was eventually decided not to include them in this publication.

TAXONOMY

Order MARSUPIALIA Illiger, 1811

Superfamily CAENOLESTOIDEA Osborn, 1910

Family GROEBERIIDAE Patterson, 1952

Groeberiidae, Patterson, 1952, p. 39.

Known Distribution: Divisadero Largo Formation, Mendoza, Argentina.

Definition: Dental formula $\overline{1{\cdot}0{\cdot}0{\cdot}4}$ or possibly $\overline{1{\cdot}0{\cdot}1{\cdot}3}$. Incisor hypselodont, very long, with axis parallel to and near the midline of the symphysis, moderately large, laterally compressed, with enamel limited to the anterior face. A diastema between the incisor and the cheek teeth. Anterior cheek tooth (M_1 or perhaps P_3) not enlarged. Cheek teeth subequal in size, rooted, not multicuspidate, without cingula, with anteroexternal paraconid. Mandible extremely short and deep with rami divergent posteriorly. Symphysis fused, steeply sloping, extending posteriorly to behind the penultimate cheek tooth, with a median posterior projection beyond the level of the last cheek tooth. Fossa for the lingual muscles prominent on the labial side of the symphysis. Coronoid process strong, projecting, arising opposite the middle part of the cheek tooth series. Masseteric fossa large, without masseteric crest. Ventral border of the horizontal ramus inflected lingually.

GROEBERIA Patterson, 1952

Groeberia, Patterson, 1952, p. 39.

Type: G. minoprioi Patterson, 1952.

Known Distribution: As for the family.

Diagnosis: Sole known member of the family Groeberiidae.

GROEBERIA MINOPRIOI Patterson, 1952

Figure 1

G. minoprioi, Patterson, 1952, p. 39.

Type: M.M.M.P. No. 738 (Coll. Scaglia), symphysis and left ramus of the mandible with right and left incisors lacking their apices, and the four left cheek teeth, the first broken and the last represented only by the roots.

Hypodigm: Type, only.

Horizon and Locality: Divisadero Largo formation, probably from level F of the section by Minoprio (1951, p. 66), about one-half kilometer east of the Cerro Divisadero Largo, Mendoza, Argentina.

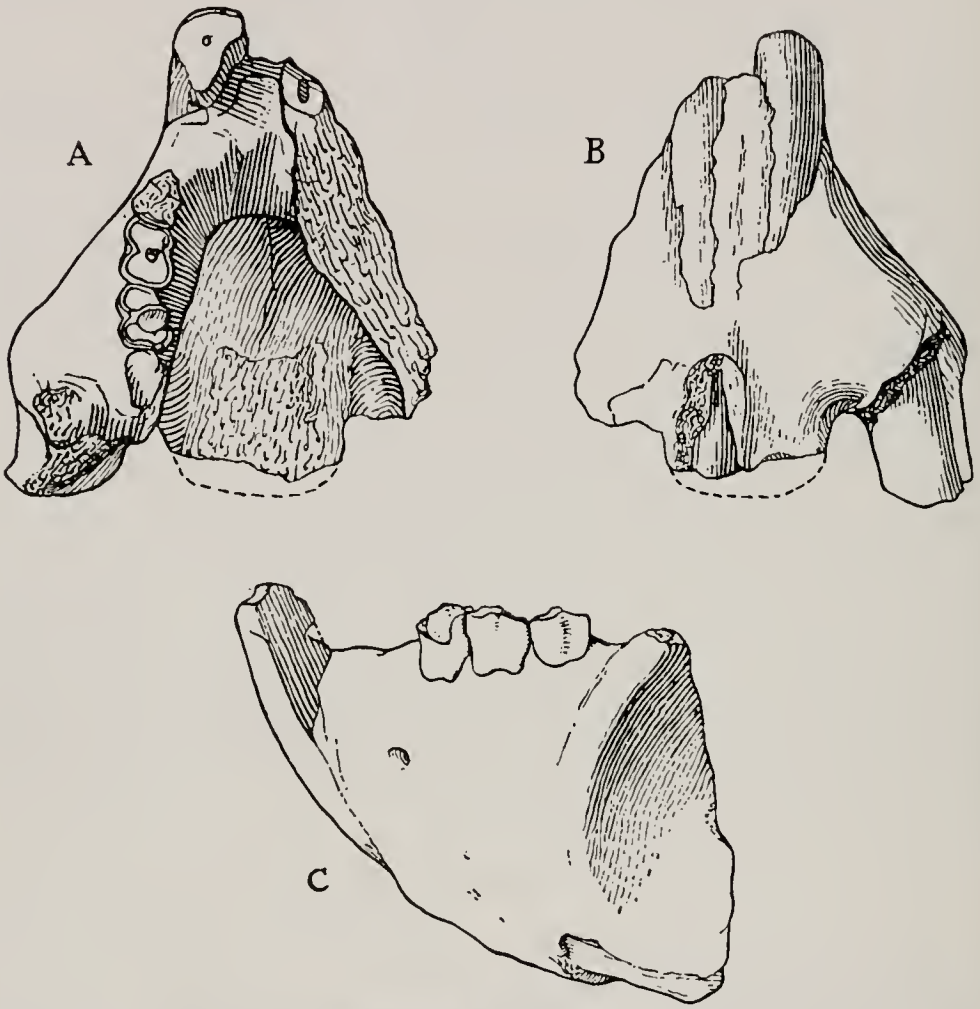

Fig. 1. *Groeberia minoprioi.* M.M.M.P. No. 738 (Coll. Scaglia), type. A, dorsal view. B, ventral view. C, lateral view. X5. (After Patterson.)

Diagnosis: Only known species of *Groeberia.*

Affinities: This extraordinary little animal is so markedly unlike anything else known that its reference to monotypic genus and family can hardly be questioned. Broader affinities are somewhat uncertain, but Patterson (1952) pointed out resemblances to various caenolestoids that justify placing it in that superfamily, especially: probably inflected angular process, enlarged procumbent lower incisor with limited enamel band, strong and salient coronoid process, simple molars suggestive of some

caenolestids and excluding close comparison with, for example, rodents or notoungulates. No new specimens are available to us, and we can add nothing to the original description and discussion by Patterson (1952).

Order LITOPTERNA Ameghino, 1889

Family ADIANTHIDAE Ameghino, 1891

Simpson and Minoprio (1949) followed Patterson (1940) and what was then a consensus in considering Ameghino's Adianthidae as a subfamily, Adianthinae, of the Macraucheniidae. We now are in agreement that family separation is justified and we therefore return the group to the rank originally given it by Ameghino. It has considerable known diversity. Four generic groups, although somewhat confused in nomenclature and definition, have been rather clearly recognized and they belong to three or more different lines of descent. The now positively recorded time range is Deseadan to Santacrucian. The resemblances to macraucheniids are real but not detailed and seem to be convergent specializations, precocious in the adianthids, rather than indications of close affinity. Any phylogenetic connection between the two groups would almost have to be pre-Casamayoran and to date from the very beginning of litoptern differentiation.

There is doubt as to the proper spelling of the name now usually applied to the type genus and consequently also as to the name of the family. The spellings are *Adianthus* and Adianthidae in the original publication, where no derivation is given. Ameghino subsequently wrote *Adiantus* and Adiantidae, with no explanation of the emendation. Palmer (1904) quoted Ameghino (evidently from a personal letter) as saying that *Adianthus* was, "Par erreur, écrire *Adiantus,* ἀδίαντος, sec." That is puzzling as the appropriateness is far from apparent and Ameghino was not ordinarily given to such a solecism as using a Greek adjective as if it were a noun. In any case, it does seem probable that the original spelling, whether correctly derived or not, was intentional and we therefore retain it — as, in fact, did Palmer in the face of Ameghino's objection. It will be noted below that neither Adianthidae nor Adiantidae may after all be an available name for this family.

ADIANTOIDES Simpson and Minoprio, 1949

Adiantoides, Simpson and Minoprio, 1949, p. 6; 1950, p. 247.

Type: A. leali Simpson and Minoprio, 1949.

Known Distribution: Divisadero Largo formation, Mendoza, Argentina.

Diagnosis: A fully brachydont adianthid litoptern with dentition somewhat similar to that of *Proadiantus* but probably closer to *Adianthus.* P^2 obliquely triangular, smaller and less transverse than P^3. P^{3-4} similar but progressively larger, strongly transverse, with persistent median internal fossette, very large and prominent parastyle, and labial face of ectoloph posterior to the parastyle excavated, with basal cingulum. Postero-internal cingulum of P^4 barely larger than antero-internal cingulum and not cuspidate or projecting to form a hypocone. Upper

Fig. 2. *Adiantoides leali.* M.H.N.M. No. 3004 P.V., type, associated skull and lower jaw. Right lateral views and crown view of lower teeth. X2. (After Simpson and Minoprio.

molars relatively transverse, with projecting parastyles and ectolophs probably relatively simple posterior to parastyles. M^{1-2} with median internal and weak postero-internal fossettes, anterior cingulum apparently small and forming no, or only a very transitory, antero-internal fossette. M^2 short anteroposteriorly, obliquely triangular. Lower cheek teeth generally more as in

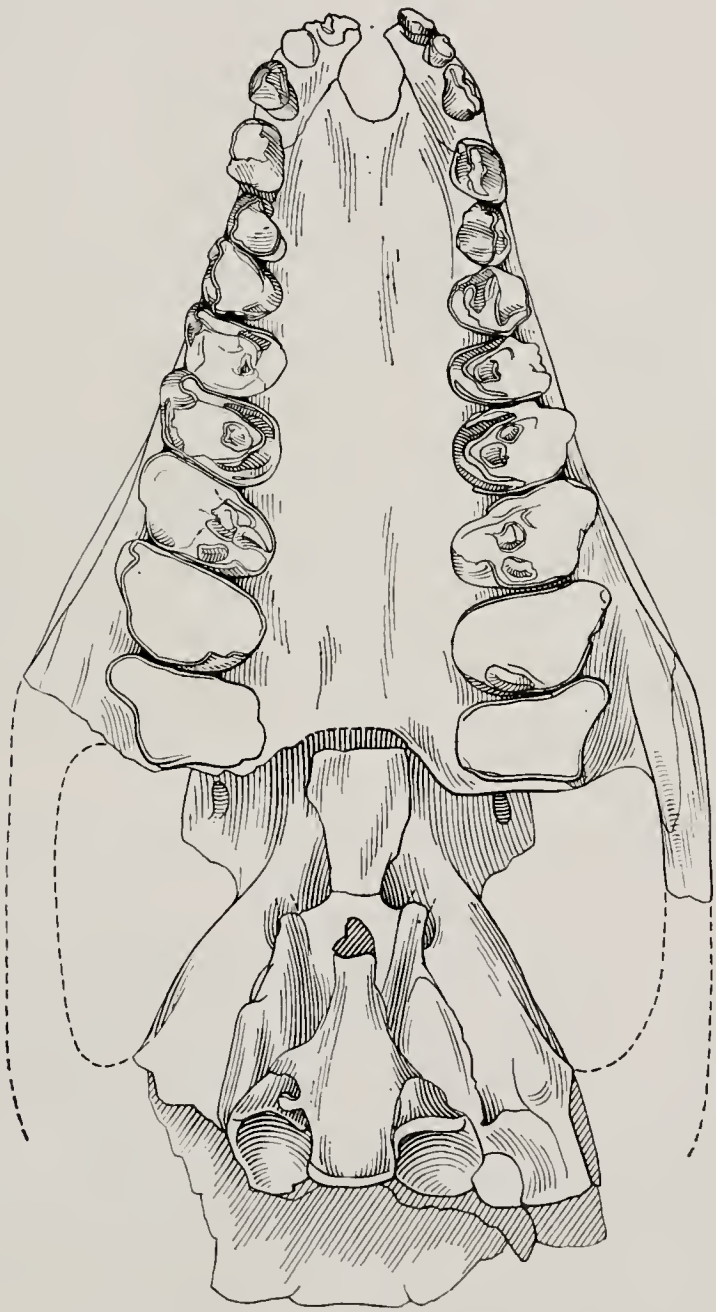

Fig. 3. *Adiantoides leali*. M.H.N.M. No. 3004 P.V., type skull. Palatal view. X2. (After Simpson and Minoprio.)

Proadiantus, but talonids on M_{1-2} shorter and narrower than trigonids and M_3 strongly distinctive in having the talonid only slightly greater than the trigonid in length and much narrower, with entoconid continuing hypoconulid crest and barely differentiated, not forming a transverse crest.

Affinities: Further (unpublished) study by Patterson since publication of Patterson (1940) and Simpson and Minoprio (1949) has revealed that the taxonomy of the Adianthidae is even more confused than previously realized and has raised several serious problems. We cannot attempt to solve or even to state those problems here, and indeed their solution probably must await discovery of better post-Deseadan specimens and perhaps also arbitrary designation of neotypes or of *nomina conservanda.* In the meantime the following conclusions, although uncertain at various points, form the basis for our present understanding of the family and of the position of *Adiantoides* in it:

Proadiantus Ameghino, 1897, Deseadan, is a valid genus and the conception of it in Patterson (1940) is essentially correct. It is on about the same level of specialization as *Adiantoides* but the two are quite distinct and represent different generic lineages.

Proheptaconus Bordas, 1936, Colhuehuapian, is based on a specimen belonging to *Adianthus patagonicus* Ameghino but it is nevertheless probably a valid genus and not a synonym of *Adianthus.* In either case it represents a third generic lineage probably not directly derivable from either *Proadiantus* or *Adiantoides.*

In the Santacrucian and perhaps but not certainly in the Colhuehuapian there is another member of this general group probably distinct from *Proheptaconus* and more nearly allied to, perhaps even derived from, *Adiantoides.* This is what we (Patterson, 1940; Simpson and Minoprio, 1949) have been calling *Adianthus* although the circumscription, exact character, and nomenclature are not as clear as we previously supposed. It is quite uncertain whether the type specimen of the type species, *Adianthus bucatus* Ameghino, 1891, really belongs to the same genus, or indeed family or order, as the subsequently referred specimens on which the concept of the genus and family have really been based. For the time being, however, we continue to call the more *Adiantoides*-like later forms *Adianthus* and the family Adianthidae.

In any case *Adiantoides* is certainly a valid genus and its affinities are clearly with forms hitherto referred to the Adianthidae whatever their correct nomenclature and definitions may prove to be. We have no additional material of *Adiantoides* and cannot otherwise add to the description and discussion in Simpson and Minoprio (1949). As there noted, *Pseudadiantus* Ameghino, 1901, certainly has nothing to do with this group and *Tricoelodus* Ameghino, 1897, is very different from *Adiantoides* and its established allies even if it might prove to have some special but considerably more remote connection.

Adiantoides leali Simpson and Minoprio, 1949

Figures 2-3

Adiantoides leali, Simpson and Minoprio, 1949, p. 10; 1950, p. 247.

Type: M.H.N.M. No. 3004 P.V. Associated skull and jaws, incomplete posteriorly.

Hypodigm: Type only.

Horizon and Locality: Divisadero Largo formation at its type locality, Mendoza, Argentina.

Diagnosis: Only known species of *Adiantoides*.

Family PROTEROTHERIIDAE? Ameghino, 1887

Phoradiadius,[1] new genus

Type: P. divortiensis (below).

Known Distribution: Divisadero Largo formation, Mendoza, Argentina.

Diagnosis: Upper molars with W-shaped ectoloph; anterior cingulum with cuspidate lingual ending anterior to protocone: protoconule, protocone, and hypocone basally united by ridge, separated by shallow notches; a pronounced fossa posterolabial to the hypocone; metaconule produced anteriorly, crista-like. Lower molars with W-shaped lophids; labial separation of trigonid and talonid V's deep, extending to lingual side of tooth: paraconid fully lingual; metaconid flattened on lingual face, with a posterior crest descending from its apex; entoconid poorly

1 Anagram of *Diadiaphorus*. We adopt one of Ameghino's devices for coining names unlikely to be preoccupied and for suggesting relationships. In this case the suggested relationship is only that the animals are litopterns and not that these two particular genera necessarily have a special connection.

or not distinguished; no talonid pillar; M_3 with simple but somewhat elongate, narrow talonid, no third lobe.

Phoradiadius divortiensis,[1] new species

Figure 4; Plate 1; Plate 2, figures *A-B*

Type: M.A.C.N. No. 18.061, part of right maxilla with imperfect M^{2-3}.

Hypodigm: Type and:

M.C.Z. No. 7407, part of right maxilla with imperfect M^3 and fragment of M^2.

M.C.Z. No. 7416, part of left lower jaw with incomplete M_2, base of M_1.

M.H.N.M. No. 3005 P.V., part of right lower jaw with unerupted M_3 (posterior end broken) and roots of M_2.

A.M.N.H. No. 45932, parts of both rami and symphysis, badly broken, left ramus through P_2 but without teeth, right ramus with part of I_3, P_{2-4} and partial alveoli or roots for M_{1-2}. Juvenile, permanent teeth just erupting.

A.M.N.H. No. 45933, part of right ramus, with M_3 (somewhat broken) erupting and roots of M_{1-2}.

A.M.N.H. No. 45931, part of left upper jaw with probable dm^{3-4} and M^1, all very poorly preserved.

A.M.N.H. No. 45930, part of left upper jaw with parts of P^3-M^3, all very poorly preserved.

Horizon and Locality: All specimens of the hypodigm are from the type area of the Divisadero Largo formation, Mendoza, Argentina.

Diagnosis: Sole known species of *Phoradiadius*.

Description: It is not absolutely certain that all specimens of the hypodigm belong to a single species, but that is sufficiently probable. All belong to litopterns of nearly the same size and suggestive of the same apparent relationships and there is no indication of more than one such litoptern in the collections. Minoprio (1947) figured a litoptern lower jaw, without tooth crowns, perhaps of this species. Simpson and Minoprio (1949) mentioned other fragmentary specimens possibly of the same form. The additional specimens now available are all poorly preserved, but on the reasonable assumption that they are conspecific they suffice to describe essential features of the dentition and to distinguish it from all genera previously adequately defined.

1 *Divortium*, "separation," for Divisadero (Largo), *-ensis*, locative suffix.

The upper premolars, P^{3-4}, of A.M.N.H. No. 45930 are too poorly preserved for useful description except to note that their squared lingual contours suggest the presence of well developed hypocones, perhaps as in *Diadiaphorus*. The presumed deciduous upper molars and the permanent molars have strongly W-shaped ectolophs. Details of structure are reasonably well shown only on M^2 of the type, but as far as preserved in the hypodigm M^1 and M^3 seem to be essentially similar except for expectable differences of proportions. On M^2 a strong anterior cingulum runs posterolingually from the ectoloph, ending in a cusplike projection anterior to the protocone. There is a sulcus between this cingulum, the protoconule, and the protocone, but no closed fossa.

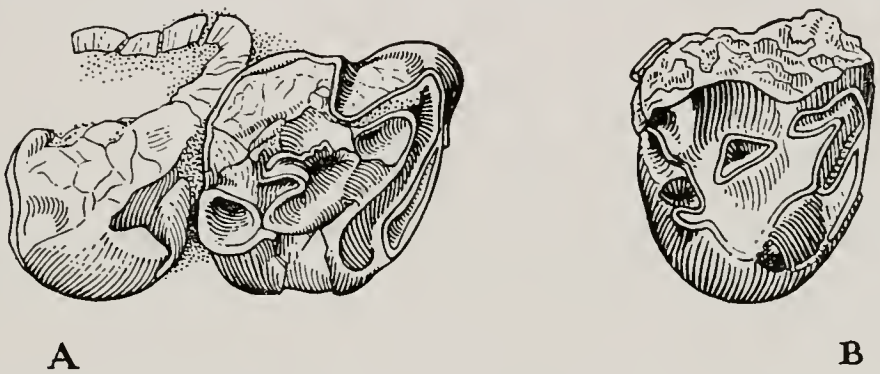

Fig. 4. *Phoradiadius divortiensis*. *A*, M.A.C.N. No. 18.061, type, right M^{2-3}. *B*, M.C.Z. No. 7407, right M^3. X2.

The slightly crescentic protocone is connected by a basal ridge to the protoconule but separated by a shallow apical notch. There is a deeper separation between the protoconule and the paracone. There is a simple and shallow central fossa between the protocone and the ectoloph. The prominent metaconule projects forward into this fossa, resembling a small crista. Protocone and hypocone are united basally and slightly separated apically as are protocone and protoconule. The hypocone also seems to be united, at least basally, with the metaconule. On the posterolingual part of the tooth there is a small but deep and prominent fossa bounded anterolingually by the hypocone. anterolabially by the metaconule, and posteriorly by a strong crest curving first posteriorly from the hypocone apex and then turning labially along the posterior margin of the tooth.

M^3 is as large as M^2, not reduced, but with the lingual contour more rounded and the hypocone considerably smaller, relatively, than on M^2.

A.M.N.H. No. 45932 has a large anterolateral tooth, the crown broken, assumed to be I_3 by comparison with proterotheres. The tooth is as large, relatively, as in any Santacrucian form and is a striking distinction from *Thoatherium*. A canine was probably present and, if so, there was virtually no diastema. P_1 was small; its crown is not preserved. P_2 is large, with a long, simple anterior blade, convex labially and excavated lingually, probably with a small anterolingual cuspule. The talonid, sharply differentiated by a labial groove, is shorter and wider. Its coronal structure is obscure. P_3 has a simple, sharp-crested, crescentic trigonid. The talonid is apparently shorter and wider, but it is badly preserved. P_4 consists of two rather simple and subequal crescents. The inner face of the metaconid is flattened and a ridge descends posteriorly from the apex. The posterior end of the tooth is somewhat broken, but it appears that the entoconid was a slight swelling at the posterolingual end of the crescent and not a distinctly separate column. It is just possible that the teeth described are P_{3-4} and M_1, but interpretation as P_{2-4} seems much more likely, on the evidence of their congruent stages of eruption (M_1 is usually fully in place when P_4 erupts) and the position of the, or the main, mental foramen beneath the anterior end of P_2.

M_3 is preserved in A.M.N.H. No. 45933 and M.H.N.M. No. 3005 P.V. Its structure is essentially like that ascribed above to P_4 except that M_3 is larger and has a somewhat more elongate, relatively narrow talonid. The paraconid is fully lingual, the posterior crest from the tip of the metaconid is again evident, and although the entoconid region is imperfect in both specimens it is clear that the entoconid did not block the lingual opening of the talonid crescent.

All teeth are fully brachydont on both labial and lingual sides.

No precise standard measurements are possible on the imperfect specimens but the median anteroposterior length of the type M^2 is about 11 mm.

Affinities: This animal is clearly a litoptern, but its affinities within that order are not entirely clear. It has many of the basic features of the Proterotheriidae and its general aspect is somewhat like *Diadiaphorus* among the well-known Santacrucian proterotheriids. When, however, details are taken into consideration the differences are so striking that they may preclude any close or special relationship. Neither *Diadiaphorus* nor any other

positively referred proterotheriid has a crista-like metaconule, a posterolingual fossa on upper molars, or so distinctly a lingually flattened and posteriorly crested metaconid. Other details in the description are also distinctive to at least a generic degree. Known pre-Santacrucian litopterns are even less similar to *Phoradiadius,* so far as comparable parts are known,[1] to such a degree that explicit comparisons would be pointless.

There is some faint possibility that *Phoradiadius* may be more nearly related to the Adianthidae, Macraucheniidae, or both, than to the Proterotheriidae. Simply bicrescentic lower cheek teeth and a tendency to form a posterior fossa on upper cheek teeth occur in some adianthids and macraucheniids. The known genera of those families are, however, all so unlike *Phoradiadius* that special relationship is improbable.

Order NOTOUNGULATA Roth, 1903

Family OLDFIELDTHOMASIIDAE? Simpson, 1945

The most abundant fossils in the collections are small, brachydont, and generally very primitive notoungulates. All resemble each other quite closely and they seem to represent a fairly compact taxonomic unit. Most of the specimens, however, fall rather clearly into three different groups and on the basis of the best materials, dentitions and skulls, these are distinctive enough that they must be placed not only in three species but also in three genera: *Allalmeia* Rusconi and two others defined as new below, *Brachystephanus* and *Xenostephanus.* All three are highly variable, and less complete specimens are often of dubious specific or generic reference. We cannot be quite certain that all the specimens listed below in the specific hypodigms are correctly placed, but the presence and distinction of the three genera are beyond serious doubt. It is possible that more than three species, or even more than three genera, are represented.

Each of the three genera now recognized has some special features, such as the enormous bullae of *Brachystephanus* and *Xenostephanus* or the peculiar upper premolars of the latter, but those peculiarities are matters of detail and all three genera come close to a picture of an entirely primitive or generalized

1 The Deseadan litopterns *Coniopternium andinum* Ameghino, 1895, *Caliphrium simplex* Ameghino, 1895, and *Notodiaphorus crassus* Loomis, 1914, appear to have been based on remains of one species close to if not in the direct ancestry of *Theosodon.* It can safely be concluded that these forms have nothing to do with *Phoradiadius.*

notoungulate. They have the characters common to all notoungulates, and they lack any of the specializations by which most of the established notoungulate suborders and families are readily recognized, even as early as the Casamayoran for some of them. Reference to the Oldfieldthomasiidae is really *faute de mieux,* based more on the absence of special characters of other defined families than on the presence of special resemblances to *Oldfieldthomasia* and other known, more surely allied early forms. Affinities are further discussed under *Brachystephanus,* below.

Although *Allalmeia* was described first, *Brachystephanus* is now best known. It will be considered first here, as more or less typifying the group, and *Allalmeia* and *Xenostephanus* will then be compared with it.

Brachystephanus,[1] new genus

Type: Brachystephanus postremus, see below.

Known Distribution: Divisadero Largo formation, Mendoza, Argentina.

Definition: Small notoungulates of primitive aspect. Dental formula $\frac{3{\cdot}1{\cdot}4{\cdot}3}{3{\cdot}1{\cdot}4{\cdot}3}$. All teeth brachydont. Incisors not or little procumbent, none particularly enlarged. Canines vertical, slightly differentiated from adjacent teeth. P^1 small, longer than wide. P^2 moderately, P^{3-4} progressively more strongly transverse. Anterior cingulum slight on P^2, stronger on P^3, and nearly equal to posterior cingulum on P^4, without cuspule on any of these teeth. Inner faces of P^{2-4} simply rounded, not quadrate or divided. Paracone and metacone barely or not distinguishable, at least when slightly worn. Strong paracone-metacone (or amphicone) fold on external face; distinct but less prominent parastyle and metastyle folds. Coronal ridges from protocone to parastyle and metastyles enclosing a single, strong, central fossette. M^{1-2} with subequal protocone and hypocone, confluent at the base, well separated by apical notch and sharp groove on lingual face. Single deep central fossa, elongate anterolabially-posterolingually; no other coronal depressions on moderately worn teeth. Crochet and cristae, if present, confluent with ectoloph after slight wear. Labial face of ectoloph with strong

1 From Greek βραχύς, short, στέφανος, crown, in allusion to the brachydont condition of the teeth, and also in parallel with *Trimerostephanos* Ameghino, another survivor of a primitive group.

paracone and metacone folds, excavated between these; parastyle moderate, metastyle slight or not distinguished, no mesostyle. Well developed, simple anterior and posterior cingula. M^3 similar but much smaller and with hypocone and metacone strongly reduced.

Lower cheek teeth as far as preserved much like a miniature *Maxschlosseria*. Possible faint twinning of metaconid on M_{1-2}, not M_3.

Bullae enormous, occupying virtually whole ventral aspect of basicranium and leaving only very narrow basioccipital-basisphenoid exposure. Porus acusticus externus comparatively large, meatus very short, crista meatus [1] not distinguishable. Occiput comparatively broad, distance between mastoid foramina equal to or greater than total depth of occiput.

Affinities: This highly distinctive genus does not particularly resemble anything previously know from Deseadan or later beds. Among earlier forms (Riochican to Mustersan), it resembles primitive members of a number of different but, at these ages, rather closely similar notoungulate families. In most cases the resemblance is just to the extent to which they and *Brachystephanus* share primitive features. Among families as recognized in Simpson (1945), the Henricosborniidae, Oldfieldthomasiidae, Archaeopithecidae, and Isotemnidae come into question, but *Brachystephanus* seems to lack the more distinct special characters of any of these families.

The extreme simplicity of the dentition, except for basic notoungulate characters, is like the Henricosborniidae, but the upper premolars are more transverse, more isotemnid-like. The strong basal fusion of protocone and hypocone, the deep, simple fossa, and the early obliteration of the crochet (if, indeed, one occurred, which is most probable as this element is virtually universal in Notoungulata) are not like the henricosborniids. On the whole, close affinities with this family are improbable. Closer comparison with the Archaeopithecidae also seems to exclude reference to that family. The molar patterns of *Brachystephanus* are much simpler in comparable stages of wear, and the archaeopithecids in Casamayoran time were already more hypsodont than the present genus.

Closest resemblance seems to be with the Oldfieldthomasiidae, on one hand, and the Isotemnidae, on the other, two families

1 We take this opportunity to correct the ungrammatical form "crista meati" previously used by Patterson and by Simpson.

quite distinct in their type genera but more or less intergrading in the known parts of some other Casamayoran representatives. Resemblances of *Brachystephanus* to either family are mostly in characters shared by both. It is, however, sharply distinct

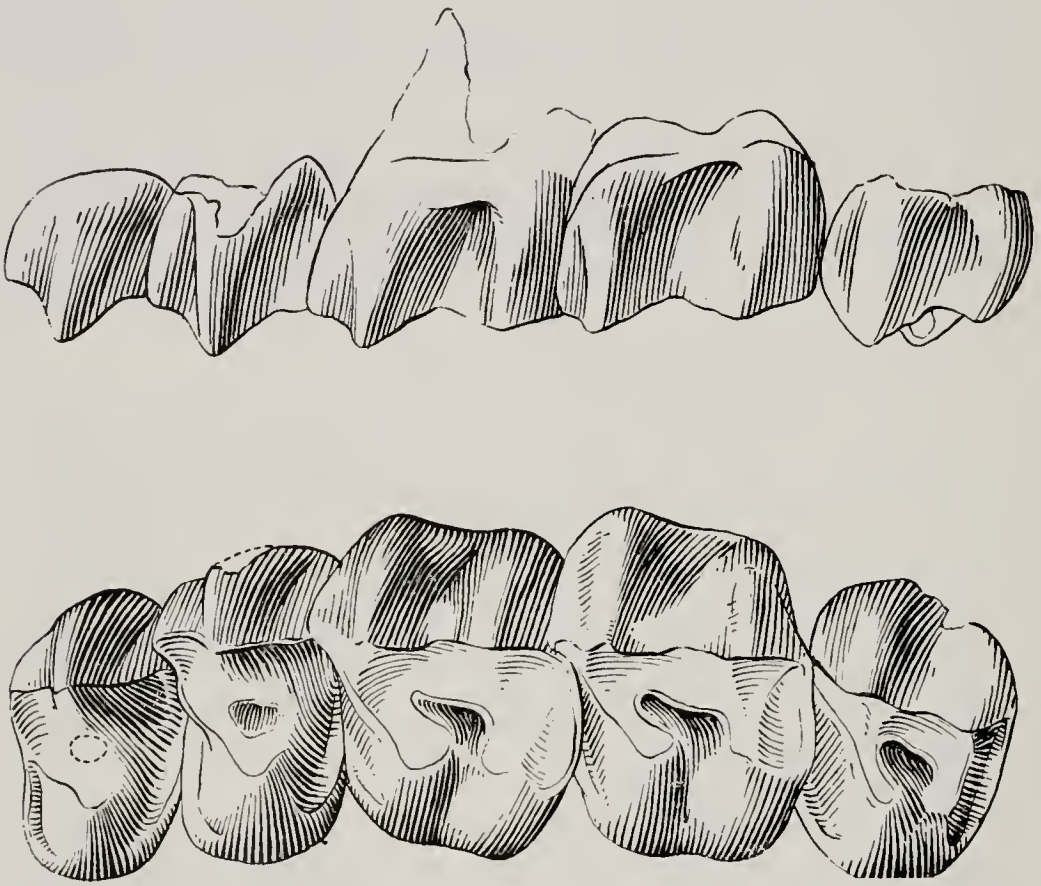

Fig. 5. *Brachystephanus postremus.* Drawn from original of A.M.N.H. No. 45946, cast of type. Left P^3-M^3, external and crown views. X about 5.

from the well-defined genera currently referred to the Isotemnidae (as listed in Simpson, 1945), and seems somewhat closer to some referred to the Oldfieldthomasiidae, particularly *Maxschlosseria*. *Brachystephanus* differs from *Maxschlosseria* in the less procumbent incisors and more differentiated canine, stronger metacone fold and weaker anterolabial fossette on the molars, and other minor particulars. The dental resemblance is, however, closer than to any other genus known to us, and in default of other evidence it is accepted tentatively as possibly indicative of relationship. Resemblance to other oldfieldthomasiids is distinctly less. The family position of *Maxschlosseria* is,

indeed, uncertain. It was referred to the Isotemnidae by Ameghino and may belong there, but reference to the Oldfieldthomasiidae seems somewhat more probable on the basis of restudy of Ameghino's specimens and of others even better (Simpson, in manuscript).

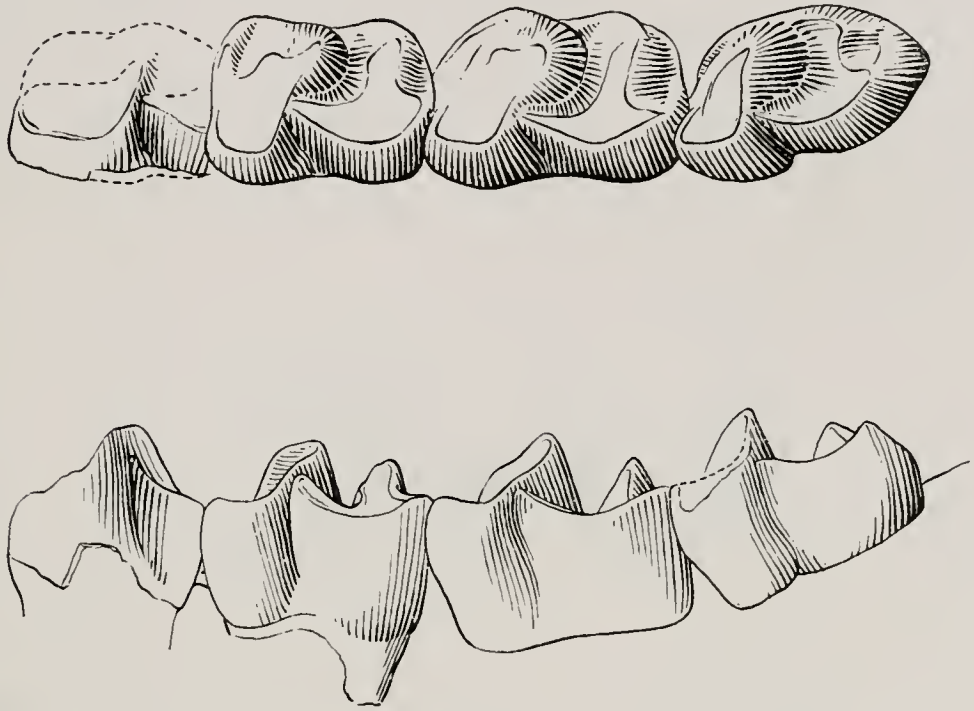

Fig. 6. *Brachystephanus postremus.* Drawn from original of A.M.N.H. No. 45946, cast of type. Left P_4-M_3, crown and external views. X about 5.

Among earlier oldfieldthomasiids, the skull is adequately known only in *Oldfieldthomasia* itself (see especially Simpson, 1936a). As far as the characters are known in both genera, the *Brachystephanus* skull is in general quite like that of *Oldfieldthomasia* and differences are almost entirely rather trivial matters of sizes or proportions of various features. That resemblance is, however, again a matter of both genera having extremely primitive, almost generalized notoungulate characters. They do differ in special details, e.g. the enormous bullae and short meatus of *Brachystephanus* or the prominent, grooved crista meatus of *Oldfieldthomasia.* There is, then, no adequate positive evidence for a special phyletic relationship between the genera. Reference of *Brachystephanus* to the Oldfieldthomasiidae is based more on negative than on positive considerations and must be accompanied by a large question mark.

Regardless of its family reference, *Brachystephanus* seems to be as primitive as any notoungulate known from the Riochican or Casamayoran but (as will be shown on a later page) its age is much later, Deseadan or immediately pre-Descadan. With its allies *Allalmeia* and *Xenostephanus*, described below, it evidently represents a late survival of a group little changed from late Paleocene or early Eocene times, but its source at those earlier times is unknown or at least not surely identified. Perhaps these late genera merit group designation at a subfamily or family level, but definition of such a group would have to be largely negative and could not, at present, clearly differentiate it from all the Casamayoran groups.

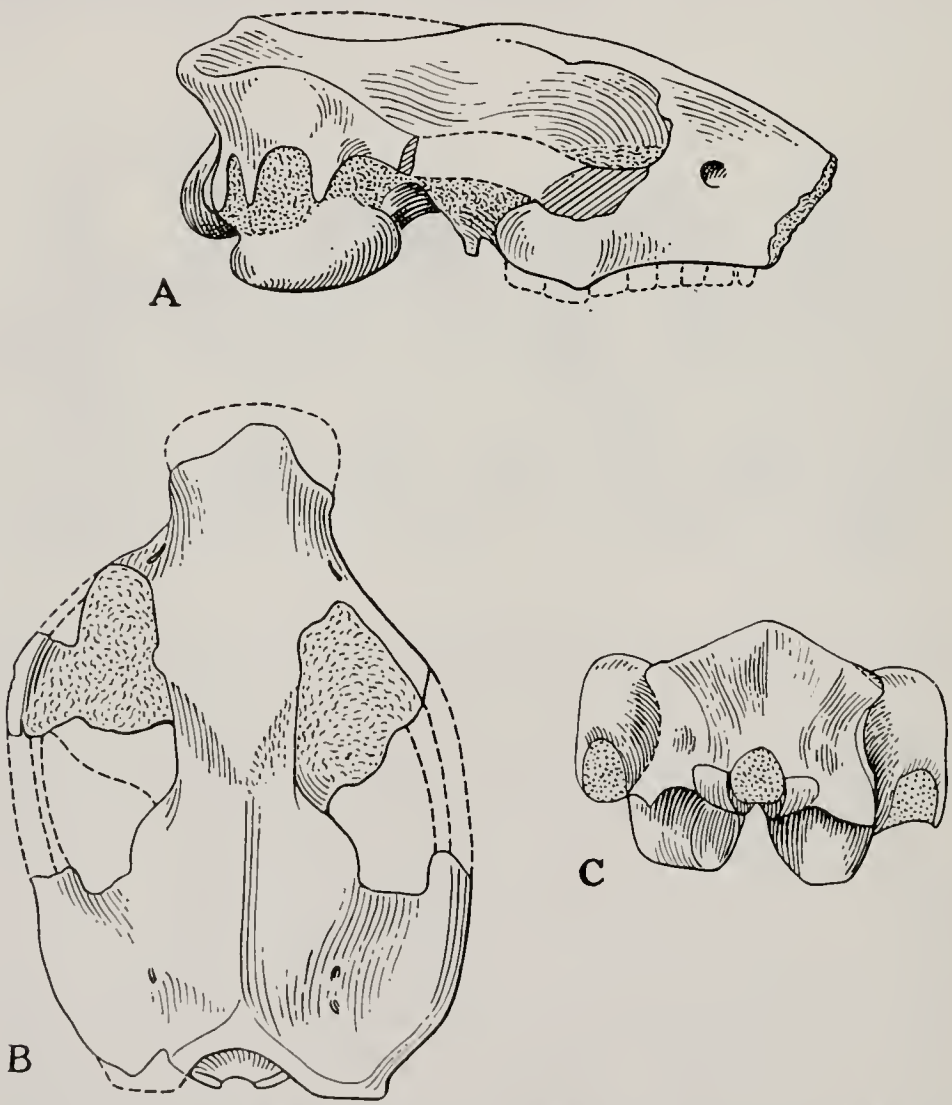

Fig. 7. *Brachystephanus postremus*. M.L.P. No. 49-XI-21-16, skull. *A*, right lateral view. *B*, dorsal view. *C*, occipital view. From sketches by Patterson. About natural size.

Table 1

Measurements in millimeters of lengths (L) and widths (W) of teeth of *Brachystephanus postremus* (*B.p.*), *Xenostephanus chiottii* (*X.c.*), and *Allalmeia atalaensis* (*A.a.*).

	P^1		P^2		P^3		P^4		M^1		M^2		M^3	
	L	W	L	W	L	W	L	W	L	W	L	W	L	W
B.p. Type			3.4	ca. 4	3.4	6.1	3.8	6.4	5.3	6.9	5.6	7.3	4.4	6.2
AMNH 45945	...	..	2.9	3.3	2.9	4.3	3.4	5.2	4.4	6.1	ca. 5	ca. 6	...	...
MLP 45-VII-10-12	...	..	3.7	...	...	...	4.1	...	4.4	...	6.0	...	...	...
X.c. Type	3.1	2.5	5.0	6.1	5.6	7.4	5.5	ca. 8	6.8	8.3	ca. 6.5	...	6.1	7.8
A.a. Type	...	..	4.0	...	3.7	6.2	4.1	7.0	5.0	7.9	5.5	9.7	5.7	ca. 9
MLP 45-VII-10-16	...	...	3.5	4.9	3.7	5.9	3.9	6.8	4.9	...	5.7	9.0	...	...
MLP 49-XI-21-21	...	...	...	...	...	...	...	...	...	...	...	...	4.9	8.6

	P_1		P_2		P_3		P_4		M_1		M_2		M_3	
	L	W	L	W	L	W	L	W	L	W	L	W	L	W
B.p. Type	...	...	...	...	...	...	3.9	2.8	4.7	3.5	5.3	3.8	5.6	3.5
AMNH 45945	...	...	...	...	3.4	1.6	3.7	2.2	4.2	3.3	4.8	3.6	ca. 5.5	ca. 3
X.c. Type	3.6	2.0	4.4	2.8	5.7	3.3	5.7	3.8	6.9	4.3	...	...	7.6	4.3
AMNH 45948	...	...	...	...	...	...	...	...	5.9	4.9	6.6	4.9	7.5	4.4
A.a. MLP 45-VII-10-9	...	...	...	...	3.4	...	3.9	3.2	4.9	3.3	6.4	3.8	...	...

Brachystephanus postremus,[1] new species

Figures 5-7; Plate 2, figures *C*-*D*; Plates 3-4

Type: A.M.N.H. No. 45946, associated partial skull and jaws with right I^{2-3}, P^{2-4}, M^{1-3}, left P^{1-4}, M^{1-3}, right lower canine, P_{3-4}, M_{1-3}, left P_{3-4}, M_{1-3} (some of these teeth incomplete), and other alveoli or roots.

Hypodigm: The type and:

A.M.N.H. No. 45945, associated partial skull and jaws with right P^{1-4}, M^{1-2}, left P^{2-4}, M^{1-2}, right P_{3-4}, M_{1-3}, left P_{1-4}, M_{1-3} (some of these teeth incomplete), and other alveoli or roots.

A.M.N.H. No. 45940, right P^3-M^3, in jaw, all badly broken.

A.M.N.H. No. 45941, left P^2-M^2, in jaw, all badly broken.

A.M.N.H. No. 45942, right P^3-M^2, in jaw, all but P^4 badly broken.

A.M.N.H. No. 45943, right P^3-M^3, in jaw, mostly broken.

A.M.N.H. No. 45944, left P^3-M^2, in jaw, all broken.

M.C.Z. No. 7408, parts of both mandibular rami with left P_4-M_2.

M.C.Z. No. 7406, badly preserved lower jaw, both rami, with broken left M_{1-3} and fragments of other teeth.

M.C.Z. No. 7409, part of left maxilla with poorly preserved P^2-M^3.

M.C.Z. No. 7410, fragment of left maxilla with incomplete M^{1-2}.

M.C.Z. No. 7411, part of right lower jaw with M_{2-3} and part of M_1.

M.C.Z. No. 7413, associated lower jaw fragments, one with right M_1 and part of M_2.

M.L.P. No. 49-XI-21-16, nearly complete skull but end of rostrum and parts of zygomatic arches missing and teeth badly broken.

M.L.P. No. 49-XI-21-22, part of right maxilla with P^2-M^3, all somewhat broken.

M.L.P. No. 45-VII-10-12, considerable part of skull, poorly preserved, with imperfect right P^2 and P^4-M^3, with associated fragments of lower jaw.

M.H.N.M. No. 3006 P.V., part of right maxilla with somewhat broken P^3-M^2.

M.H.N.M. No. 3007 P.V., fragment of left maxilla with broken M^2 and complete M^3.

Horizon and Locality: Divisadero Largo formation, 8 kilometers west of the city of Mendoza, Argentina.

1 Latin, *postremus*, latest, in reference to the late occurrence of so primitive a notoungulate.

Diagnosis: Sole named species of the genus as defined above. Measurements in Table I.

Description: The dentition is adequately characterized in the generic diagnosis and the figures, so that tooth-by-tooth description is unnecessary.

Considerable parts of the skull are present in A.M.N.H. No. 45946 (a cast of the type, collected by Minoprio), A.M.N.H. No. 45945 (also collected by Minoprio), M.L.P. No. 45-VII-10-12 (collected by Chiotti), and M.L.P. No. 49-XI-21-16 (collected by Antonio Castro). In detail these specimens are disappointing, because parts grossly present are nevertheless badly distorted and fragmented. It seems to be a characteristic of the Divisadero Largo that its fossils are often preserved rather as a mosaic of fragments than in the original state, and that enamel, especially, but also often dentine and bone tend to pulverize and spall off in almost explosive fashion on exposure. Nevertheless, comparison of the four specimens reveals much of the essential skull structure.

No specimen has the tip of the rostrum complete, but the face was clearly rather short, with the anterior border of the orbit, which is above P^4, well anterior to the midpoint of skull length. The rostrum narrows markedly in the premolar region, expands again slightly at the canines, and is truncate across the arcuate but largely transverse incisor series. The narrow nasals were not retracted. The infraorbital foramen is above P^{2-3} and the anterior root of the zygomatic arch is above M^{1-2}. The orbit, of moderate size, has a broad floor but is completely open posteriorly. There is no distinct postorbital constriction and, as shown in a partial natural endocranial cast in A.M.N.H. No. 45945, the olfactory bulbs are large, fully exposed dorsally, and as wide as the anterior parts of the cerebrum. The cerebrum widens posteriorly and is followed by a slightly narrower, broadly exposed cerebellum of almost equal length. The single sagittal crest became rather high and sharp in adults. The zygoma, although not complete in any specimen, seems to have been normal (lacking, e.g., the characteristic interatheriid specialization of the jugal).

Reference has been made in the generic diagnosis to the enormous pear-shaped bullae, which occupy virtually the whole ventral aspect of the basicranium. The porus acusticus externus, at the posterolateral end of the bulla, is comparatively very large and is extraordinarily posterior and ventral in position,

only a little anterior to the level of the condyles and quite as low in its lower part. The meatus is so short as to be virtually nonexistent, in sharp contrast to the transversely elongate, anteroposteriorly pinched meatus of most specialized notoungulates. The porus faces posterolaterally. The anterior edge of the porus is elevated and liplike, running into and hardly distinct from the postglenoid process. No distinct crista meatus is present, an absence also peculiar but not unique and possibly primitive for a notoungulate. The usual notoungulate epitympanic inflation of the squamosal is present and strongly marked, but the epitympanic sinuses are here surpassed in size by the large bullae.

The occiput consists of a central portion or occiput proper and of the more lateral, large posterior faces of the epitympanic inflations. Between the two is a groove which seems to have contained a mastoid foramen, mastoid exposure, and "posterior adventitious bone" much as in *Oldfieldthomasia* (Simpson, 1936a, and see also Patterson, 1936). The occiput proper, relatively broad as noted in the generic diagnosis, is convex just above the large, almost circular foramen magnum, but is excavated medially above that and also laterally on each side.

Xenostephanus,[1] new genus

Type: Xenostephanus chiottii, see below.

Known Distribution: Divisadero Largo formation, Mendoza, Argentina.

Diagnosis: Small notoungulates of generally primitive aspect, dentition similar to *Brachystephanus* except as follows. P^1 small and simple, protocone incipient. P^{2-4} with strong, basined anterior and posterior cingula. P^{3-4}, at least, with distinct anteromedian cuspule, on P^3 dependent on the cingulum and on P^4 with a separate, low crest running to the parastyle. P^{2-4} with posterior loph from protocone to ectoloph, but no anterior loph and no closed fossa. Buccal face of ectoloph somewhat less deeply excavated between paracone and metacone, and internal groove between protocone and hypocone less strong. Metacone fold vestigial on M^3. Talonid lophids on P_{2-4} running to apex of metaconid on lingual side of tooth rather than abutting against base of trigonid medially. On M_3 metaconid distinctly bifid at apex and entoconid not distinctly crested transversely.

1 Greek ξένος, strange, στέφανος, crown, in allusion to the upper premolar crowns, peculiar among notoungulates, and in euphony with *Brachystephanus.*

Bullae very large and occiput relatively broad, both about as in *Brachystephanus*. Porus acusticus externus much smaller. Meatus short but more distinct than in *Brachystephanus* and

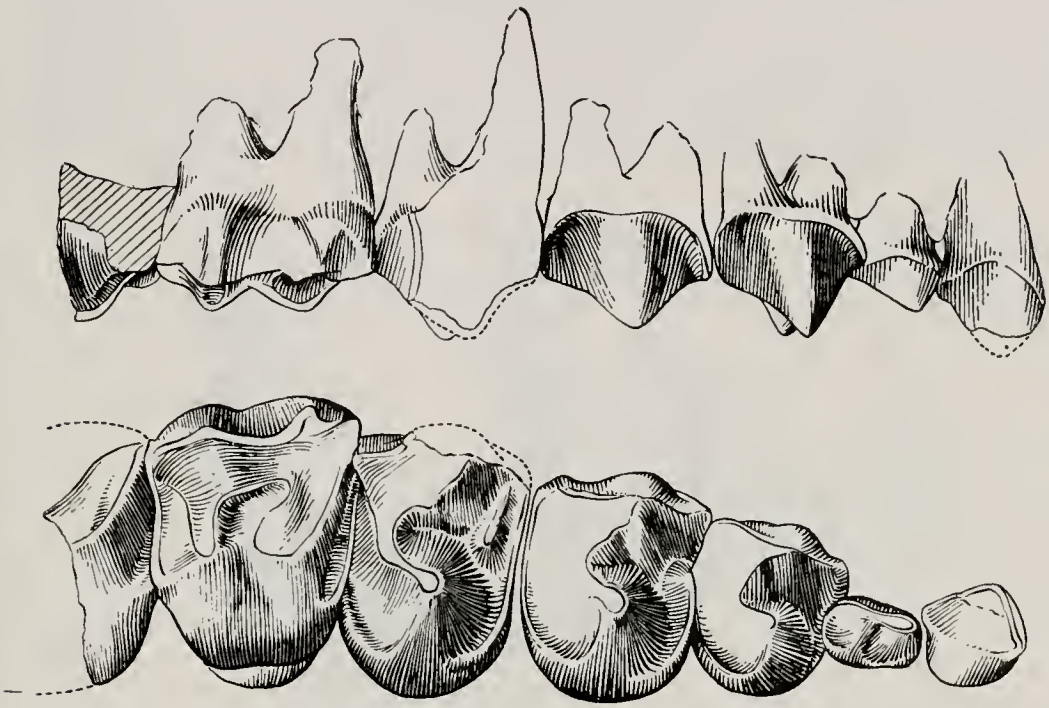

Fig. 8. *Xenostephanus chiottii*. Drawn from original of A.M.N.H. No. 45947, cast of type. Right C-M^2, labial and crown views. X about 3.

with a feeble crista meatus, which is, however, poorly differentiated from the postglenoid process. Paroccipital process probably considerably stronger than in *Brachystephanus*. Proportions of the occiput as in the latter genus.

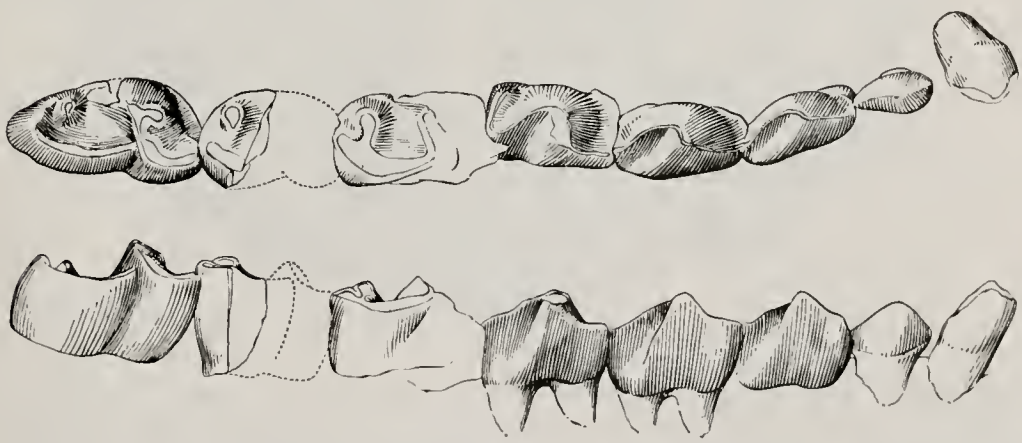

Fig. 9. *Xenostephanus chiottii*. Drawn from original of A.M.N.H. No. 45947, cast of type. Right C-M_3, crown and labial views. X about 3.

Affinities: *Xenostephanus* has much the same resemblances to (presumably) earlier families as has *Brachystephanus*. The most distinctive teeth, the upper premolars, are, however, quite different from those of *Brachystephanus* and at least equally distant from those of any other genus known to us. They are, for instance, decidedly less like *Maxschlosseria* than are the corresponding teeth of *Brachystephanus*. Among such simple and primitive notoungulate dentitions, differences of this degree may

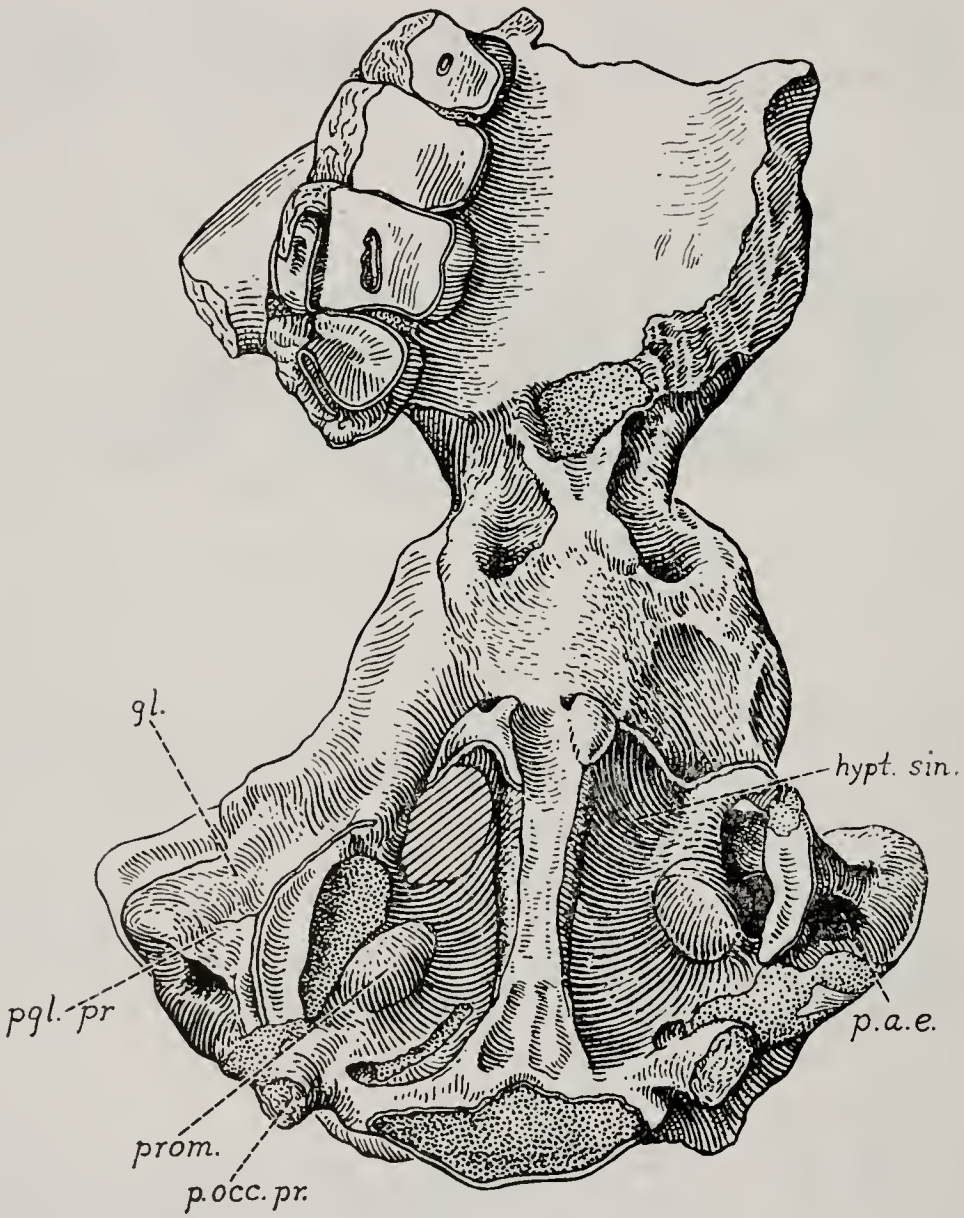

Fig. 10. *Xenostephanus chiottii.* M.H.N.M. No. 3008 P.V., incomplete skull. Ventral view. *gl.*, glenoid fossa; *hypt. sin.*, hypotympanic sinus; *p.a.e.*, porus acusticus externus; *pgl. pr.*, postglenoid process; *p. occ. pr.*, paroccipital process; *prom*, promontorium. X2.

reflect pertinence to wholly distinct families or even higher categories. The dental resemblance to *Brachystephanus* is, nevertheless, considerable, and no other definite affinities are suggested. The skulls are closely similar as far as known, except for the definite but small differences in the ear region noted in the diagnosis. *Xenostephanus* and *Brachystephanus* may be tentatively considered as divergent generic lines of the same general stock, perhaps survivors of a lineage near or in the Oldfield-thomasiidae, as already suggested for *Brachystephanus*.

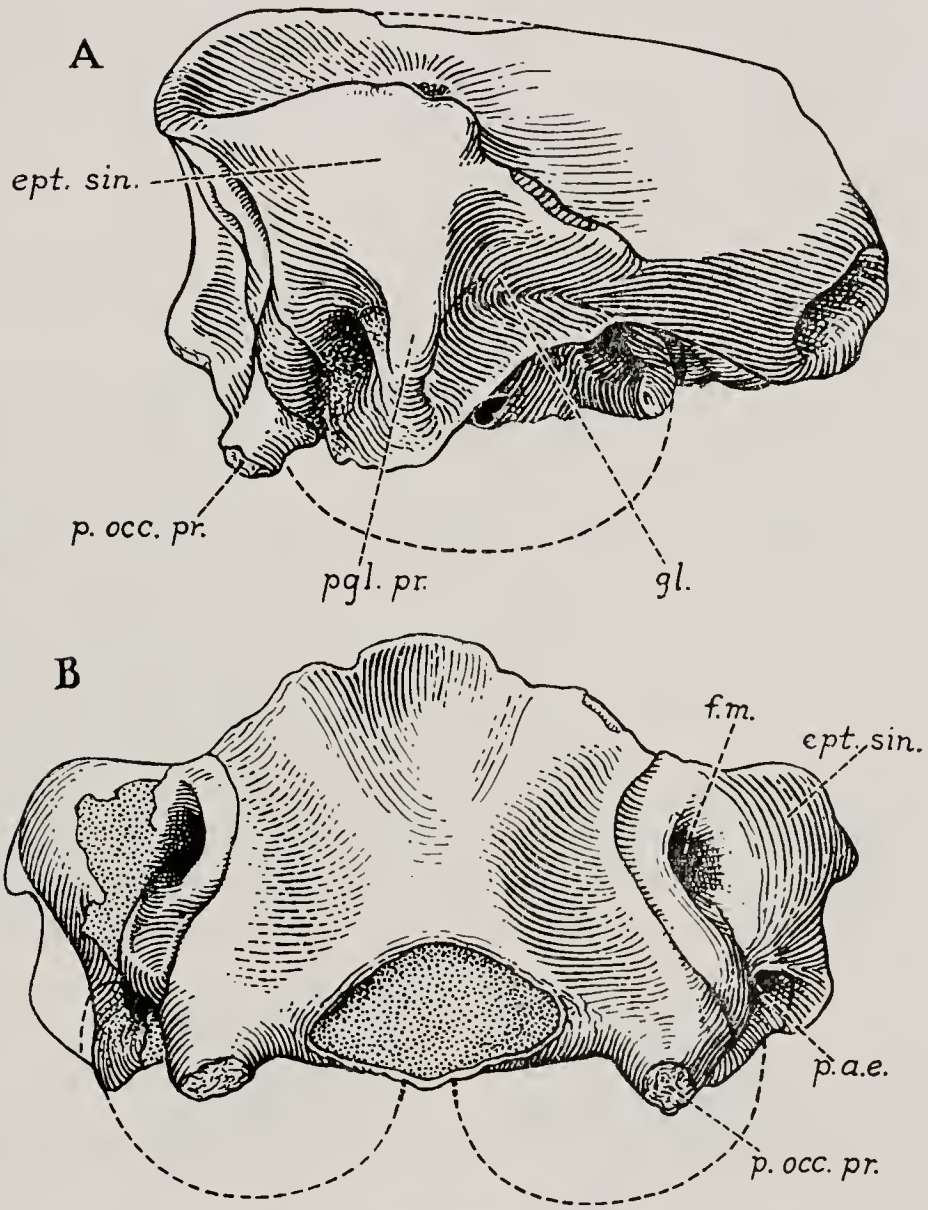

Fig. 11. *Xenostephanus chiottii*. M.H.N.M. No. 3008 P.V., incomplete skull. *A*, right lateral view of cranium. *B*, occipital view. *ept. sin.*, epitympanic sinus; *f.m.*, mastoid foramen; *gl.*, glenoid fossa. *p.a.e.*, porus acusticus externus; *pgl. pr.*, postglenoid process; *p. occ. pr.*, paroccipital process. X2.

Xenostephanus chiottii,[1] new species

Figures 8-11

Type: A.M.N.H. No. 45947, partial skull and jaws with right upper C, P^{1-4}, M^{1-2}, left upper C, P^{1-4}, M^{2-3}, right lower C, P_{1-4}, M_{1-3}, left lower C, P_{1-4}, some of these teeth incomplete.

Hypodigm: Type and:

A.M.N.H. No. 45948, left lower jaw with C, P_{1-4}, M_{1-3}, some teeth broken.

M.L.P. No. 49-XI-21-20, fragment of left lower jaw with M_{2-3}.

M.C.Z. No. 7415, numerous small fragments of upper and lower jaws with identifiable parts of right P^4-M^1.

M.H.N.M. No. 3008 P.V., most of cranium and part of right maxilla with imperfect P^4-M^3.

Horizon and Locality: Divisadero Largo formation, 8 kilometers west of the city of Mendoza, Argentina.

Diagnosis: Sole known species of the genus as defined above.

Description: Little needs to be added to the points given in the generic definition or visible in the figures.

The skull is fairly well known between the type (specimen found by Minoprio of which A.M.N.H. 45947 is a cast) and M.H.N.M. No. 3008 P.V. (also collected by Minoprio). There is a definite postorbital constriction, more distinct than in *Brachystephanus*. The epitympanic sinus is well developed, but is probably relatively smaller than in *Brachystephanus*. The mastoid foramen and "posterior adventitious element," much as in *Oldfieldthomasia*, are more clearly visible in M.H.N.M. No. 3008 P.V. than in our materials of *Brachystephanus*, but the two genera probably do not differ significantly in this respect. The comparatively extremely small porus acusticus externus of *Xenostephanus* faces even more posteriorly than in *Brachystephanus* and suggests that the external ear was peculiar in some unknown way.

Allalmeia Rusconi, 1946

Allalmeia Rusconi, 1946a, (unnumbered page); 1946b, p. 18.

Type: Allalmeia atalaensis Rusconi, 1946.

Known Distribution: Divisadero Largo formation, Mendoza, Argentina.

1 For Dr. Olivo Chiotti, in recognition of his stratigraphic studies of the Divisadero Largo and adjacent formations.

Definition: (Redefinition by the present authors.) Small notoungulates of primitive aspect. Dental formula $\frac{3\cdot1\cdot4\cdot3}{3\cdot1\cdot4\cdot3}$. Dentition closely similar to that of *Brachystephanus* but differing in detail. Canines poorly differentiated. P^1 very small. P^2 abruptly larger, triangular. P^{3-4} with well developed protocone-parastyle loph and forming deep, closed fossette in early wear stages. M^{1-3} with strong, approximated parastyle and paracone ridges on buccal faces; metacone ridge present but less distinct. Buccal face with basal cingulum between paracone and metacone, deeply excavated and forming small buccal fossette above flattened ectoloph face. Protocone and hypocone well separated above base. Base on lingual side broad, somewhat flattened and shelflike. Strong anterior cingulum with tendency to extend around protocone to lingual face. Approximately equal posterior cingulum, shorter,

Fig. 12. *Allalmeia atalaensis.* M.H.N.M. No. 507 P.V., type. Copy of sketch by Patterson of crown view of right upper teeth. X about 1.5.

ending lingually posterior to hypocone. M^3 relatively larger than in *Brachystephanus* or *Xenostephanus;* metacone and metaloph reduced, metaloph not completely fused with small hypocone at lingual end. Crista obliqua of lower premolars abutting against base of metalophid, not running to metaconid.

Bullae relatively smaller than in *Brachystephanus* and *Xenostephanus,* leaving fairly wide medial basioccipital-basisphenoid exposure and not extending to posterior end of basicranium.

Fig. 13. *Allalmeia atalaensis. A,* M.L.P. No. 49-XI-21-21, right M^{2-3}, copy of sketch by Patterson. *B,* M.C.Z. No. 7412, left M^{2-3}. X2.

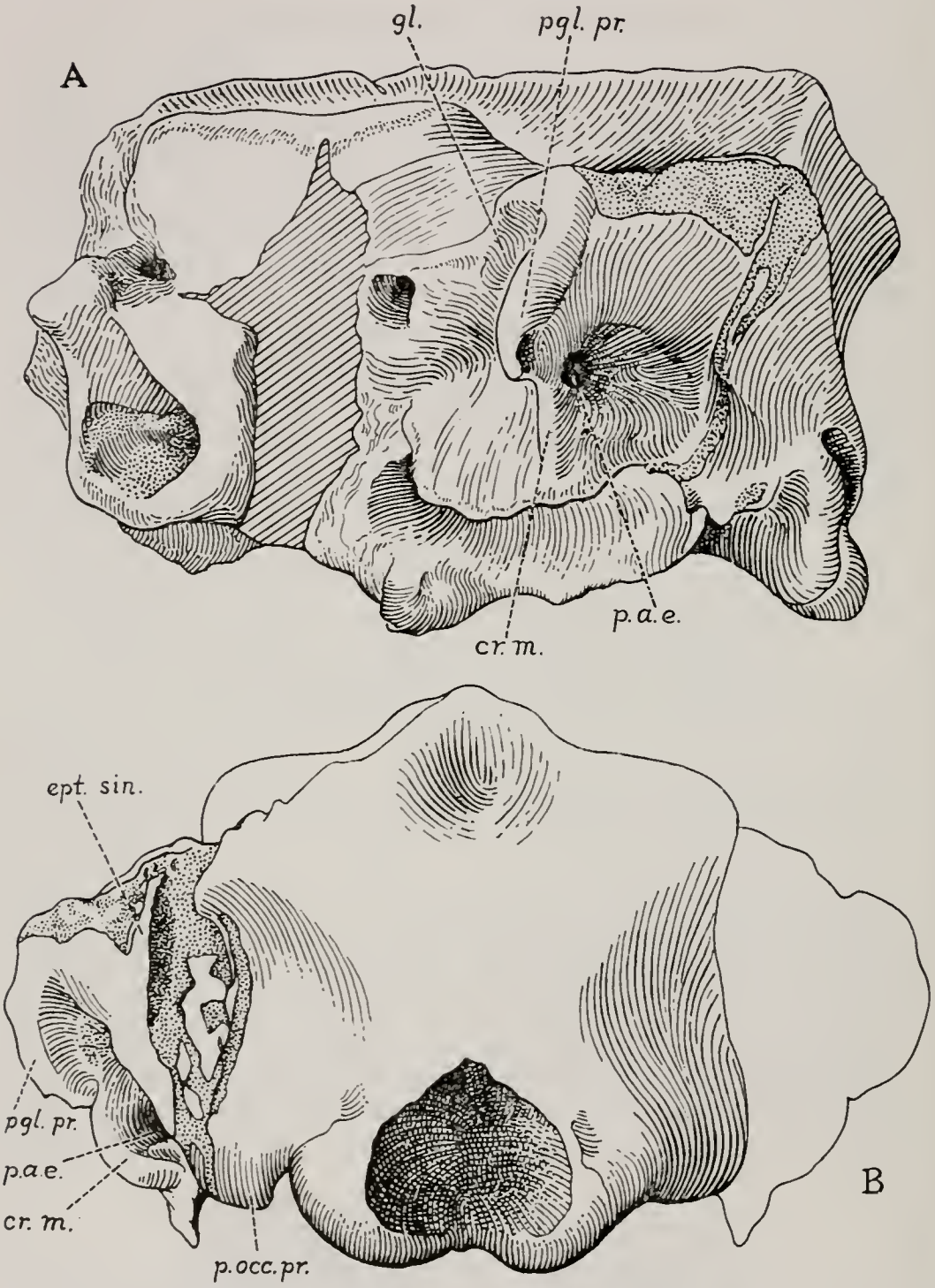

Fig. 14. *Allalmeia atalaensis.* M.H.N.M. No. 3009 P.V., cranium. *A*, left lateral view. *B*, occipital view. *cr. m.*, crista meatus; *ept. sin.*, epitympanic sinus; *gl.*, glenoid fossa; *p.a.e.*, porus acusticus externus; *pgl. pr.*, postglenoid process; *p. occ. pr.*, paroccipital process. X2.

Porus acusticus externus small, but relatively slightly larger than in *Xenostephanus*. Distinct but short meatus, relatively longer than in *Xenostephanus*, and simple crista meatus also somewhat better developed than in that genus, running to postglenoid process but offset from it. Occiput relatively higher and narrower, distance between mastoid foramina less than total height of occiput.

Comments and Affinities: Our concept of *Allalmeia* is different from that of Rusconi (1946a, b) as a consequence of restudy with more specimens and more extensive comparative materials. As regards the dentition, the most important emendation is the observation that the apparent coronal outlines of the upper cheek teeth in Rusconi's figures are found to represent the root

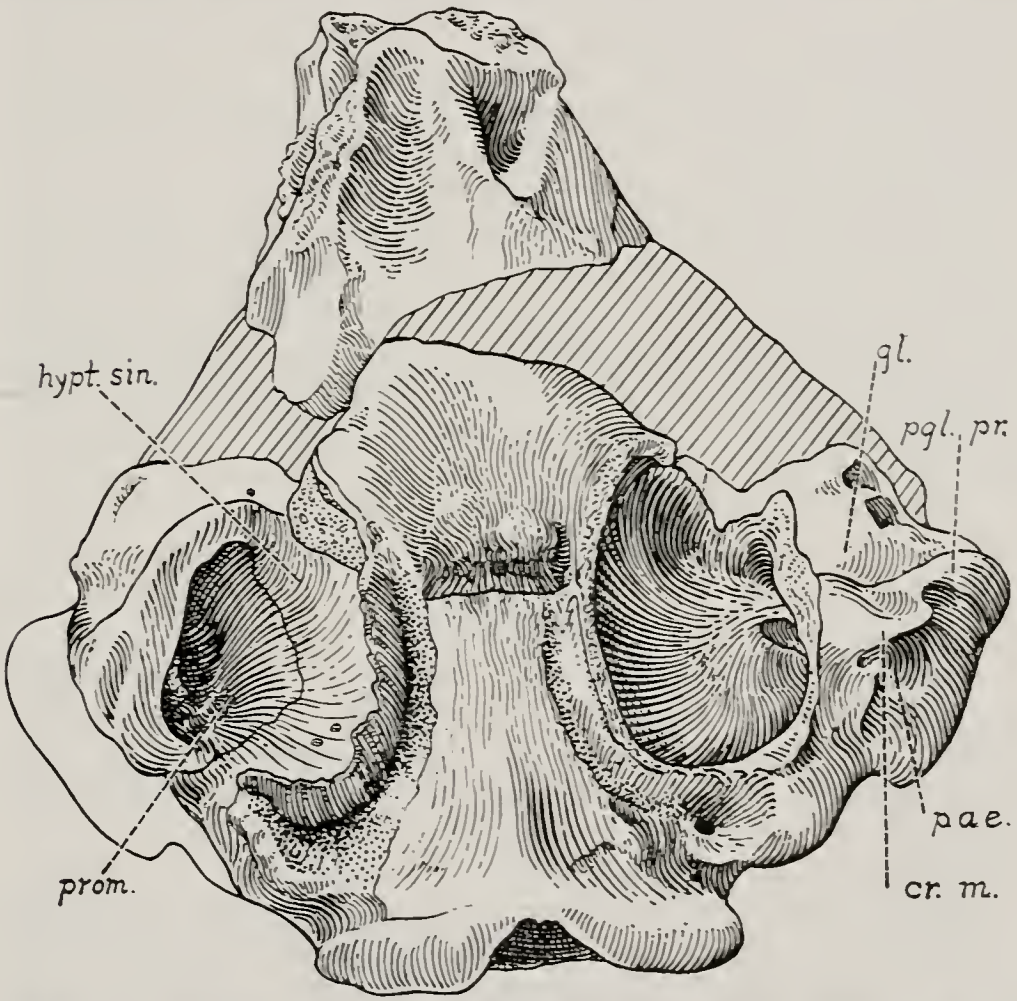

Fig. 15. *Allalmeia atalaensis*. M.H.N.M. No. 3009 P.V., cranium. Ventral view. *cr. m.*, crista meatus; *gl.*, glenoid fossa; *hypt. sin.*, hypotympanic sinus; *p.a.e.*, porus acusticus externus; *pgl. pr.*, postglenoid process; *prom.*, promontorium. X2.

bases, not the crowns proper, which are almost entirely broken away on all the teeth of Rusconi's specimen. The true coronal outlines are angulate as in all primitive notoungulates and not rounded buccally as shown in the original type figure. The dental formula was not correctly inferred from the type, alone. Like its allies in this fauna, *Allalmeia* has the full placental formula. Our additional specimens also reveal other dental and cranial characters not preserved in the type.

The original provisional reference of *Allalmeia* to the Notostylopidae is certainly incorrect. *Allalmeia* has none of the clear-cut characters diagnostic of that primitive but not generalized family. *Allalmeia* resembles its faunal associates *Brachystephanus* and *Xenostephanus* much more than it does any other known genera. The differences, while demanding generic separation, are not profound. Resemblance to *Brachystephanus* is especially close, and *Allalmeia* will probably find its correct taxonomic place next to that genus. For the present, then, and in a strongly provisional way it is likewise placed in the Oldfieldthomasiidae? with a decided question mark.

Rusconi's original specimen includes numerous associated elements of the postcranial skeleton. Like the teeth and skull, they have the characters of a very primitive, generalized notoungulate and lack diagnostic peculiarities of any of the contemporaneous or later families. Comparable parts are not known in the earlier Oldfieldthomasiidae and the skeleton does not, at present, cast any further light on affinities.

Allalmeia atalaensis Rusconi, 1946

Figures 12-15

Allalmeia atalaensis Rusconi, 1946a (unnumbered page); 1946b, p. 18.

Type: M.H.N.M. No. 507 P.V., palate and lower jaw with most of the teeth (poorly preserved) and parts of associated skeleton.

Hypodigm: Type and:

M.L.P. No. 45-VII-10-9, symphysis and parts of mandibular rami with poorly preserved left C-M_1 and right P_3-M_3.

M.L.P. No. 45-VII-10-10, part of right maxilla with imperfect P^3-M^3.

M.L.P. No. 45-VII-10-16, part of left maxilla with imperfect P^2-M^3.

(The three preceding M.L.P. specimens probably all belong to the same individual, collected by Chiotti.)

M.L.P. No. 49-XI-21-21, fragment of right maxilla with M^3 and part of M^2.

M.C.Z. No. 7412, fragment of left maxilla with M^{1-2} and part of M^3.

M.H.N.M. No. 3009 P.V., cranium and associated right maxilla with very poorly preserved P^3-M^3 and much of lower jaw with very poorly preserved left P_4-M_3 and roots of anterior teeth on both sides.

Horizon and Locality: Divisadero Largo formation (type locality and Papagallos). Mendoza, Argentina.

Diagnosis: Sole named species of the genus as defined above.

Description: The generic diagnosis and the general similarity to *Brachystephanus* obviate the need for detailed description. Preservation of the teeth is bad in almost all instances, but comparison of all the specimens leaves little doubt of the essential characters. Most of our precise knowledge of dentition and skull comes from specimens other than the type, and as there is much variation among the specimens this leaves possible slight doubts as to identification. The cranium is known only from M.H.N.M. No. 3009 P.V., the poorly preserved dentition of which has been directly compared with the type. There are, of course, differences but they are so slight as not to warrant specific separation. As noted in the generic diagnosis, known differences in dentition from *Brachystephanus*, and in cranium from *Xenostephanus*, are matters of relative proportions or of structural details and are not fundamental or striking.

The known postcranial parts of the type, adequately described by Rusconi (1946b), are slender, in keeping with the small size of the animal, but show no evident specializations. The pes is pentadactyl and more or less mesaxonic, but with digit IV longer than II. Except in proportions generally correlated with weight, the skeleton is almost as in Casamayoran Isotemnidae (see Simpson, 1936b). One apparent difference, the great proximodistal elongation of the third trochanter, shown in the figure of the femur (Rusconi, 1946b, fig. 18), perhaps is not real. The specimen is imperfect in this region and is largely restored in the figure.

Family MESOTHERIIDAE Alston, 1876

Subfamily TRACHYTHERINAE Simpson, 1945

TRACHYTHERUS? Ameghino, 1889

TRACHYTHERUS? MENDOCENSIS Simpson and Minoprio, 1949

Figures 16-17

Trachytherus mendocensis, Simpson and Minoprio, 1949, p. 18; 1950, p. 249.

Type: M.H.N.M. No. 2494 P.V., right P^{2-3}, M^1, and parts of right M^2 and left P^2-M^1.

Hypodigm: Type and:

M.L.P. No. 45-VII-10-2, Chiotti Collection, right M^3.

Horizon and Locality: Type Divisadero Largo formation, Mendoza, Argentina.

Diagnosis: Much smaller than other species referred to *Trachytherus;* type M^1 9.1 mm long and 8.3 mm wide on grinding surface. P^{2-3} strongly transverse, obliquely triangular in section,

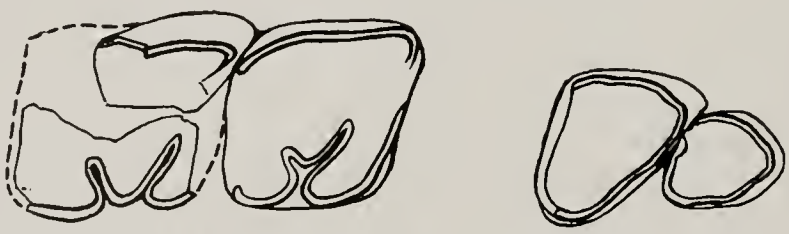

Fig. 16. *Trachytherus? mendocensis.* M.H.N.M. No. 2494 P.V., type, right P^{2-3}, M^{1-2}, crown view. X2. (After Simpson and Minoprio.)

without grooves or ridges on rounded outer face. M^1 trapezoidal in section, almost as wide as long in middle wear stage, outer face smoothly curved. M^{2-3} more angulate anteroexternally. M^3, at least, with less basal widening and diminution of lingual fold and lobe than in *T. spegazzinianus.*

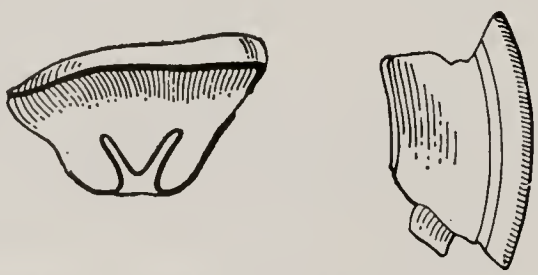

Fig. 17. *Trachytherus? mendocensis.* M.L.P. No. 45-VII-10-2, right M^3, crown and anterior views. Copy of sketch by Patterson. X2.

Affinities: The previously undescribed M^3 in the Chiotti Collection almost certainly belongs to this species, and it adds somewhat to the characterization. The animal is clearly a trachytherine, and the available material does not permit clear-cut generic distinction from *Trachytherus*, which is not to say that it can be positively referred to that genus. We, therefore, modify the original designation by putting a question mark after the generic name. We suspect that further material will force generic separation, as suggested by wide specific separation from the type species of *Trachytherus*.

Family HEGETOTHERIIDAE Ameghino, 1894

Subfamily HEGETOTHERIINAE Ameghino, 1894

ETHEGOTHERIUM,[1] new genus

Type: Prohegetotherium carettei Minoprio, 1947.

Known Distribution: Divisadero Largo formation, Mendoza, Argentina.

Diagnosis: Hegetotheres resembling *Prohegetotherium* but with anterior teeth slightly separated rather than appressed; canines in arc formed by cheek teeth, not buccal to it; P_1^1 smaller and less elongate than in *Prohegetotherium;* external grooves on upper molars median, not anterior, on ectoloph; P_2 relatively shorter; lobes of lower cheek teeth rounded rather than angular; anteroposterior axes of those teeth in sequence, not overlapping shingle-like as in *Prohegetotherium;* talonid of M_3 without external groove and with internal groove fainter than in *Prohegetotherium.*

Affinities: Comparisons made by Minoprio (1947) and Simpson and Minoprio (1949) were impeded by the inadequate and in part incorrect available data on the genotype of *Prohegetotherium, P. sculptum.* The type material of that species has now been restudied by Patterson, and a lower dentition almost certainly of the same species has been described and figured by Chaffee (1952). Adequate comparisons can, therefore, now be made for the first time. As indicated in the preceding diagnosis, the dentition of *"Prohegetotherium" carettei* proves to be markedly different from that of typical *P. sculptum.* It is, of course, uncertain whether these characters are quite constant

1 Anagram of *Hegetotherium.*

or will be found in all species that might eventually be referred to *Ethegotherium*, but there can be no doubt that in sum they warrant generic rank. *Ethegotherium* differs about as much from *Prohegetotherium* as the latter does from *Hegetotherium*. The reduction of posterior incisors, canines, and anterior premolars and the development of diastemata in that region seem to be a progressive, rodent-like specialization in *Hegetotherium* (and later hegetotheres). In that respect, *Ethegotherium* is distinctly more specialized than *Prohegetotherium* but less than *Hegetotherium*. Imbrication of the lower cheek teeth would also seem to be a specialization, apparently at least as advanced in *Prohegetotherium* as in *Hegetotherium* and absent in *Ethegotherium*. In some other characters such as the contours of the ectolophs and of the talonid of M3, the three genera are distinct and divergent, without its being clear that one condition is more primitive or more specialized than another.

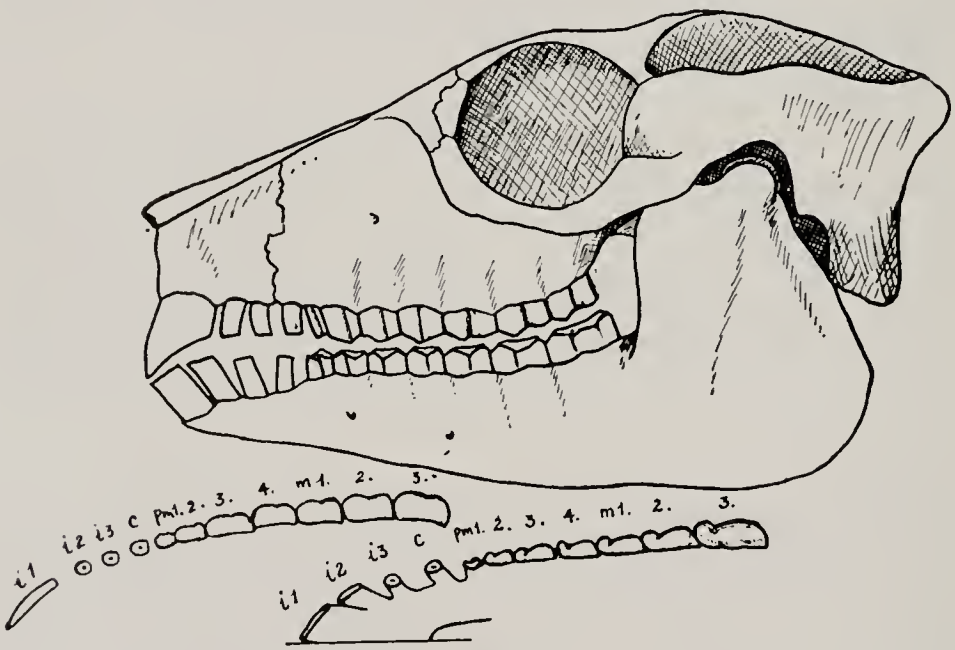

Fig. 18. *Ethegotherium carettei*. M.A.C.N. No. 16609, type, skull and jaws. Reconstructed left lateral view and crown outlines of upper and lower teeth. X1. (After Minoprio.)

Prohegetotherium may be somewhat nearer the ancestry of *Hegetotherium* than is *Ethegotherium*, but it is unlikely that known species of either of the earlier genera are directly ancestral to known species of *Hegetotherium*. The affinities of *Ethegotherium* are clearly in this group, the Hegetotheriinae, and not with

Pachyrukhos, Prosotherium, and other genera of different subfamilies in the Hegetotheriidae. Unfortunately, useful comparison cannot be made with the Mustersan *Eohegetotherium,* the only supposed hegetotheriine so far named from pre-Deseadan beds. Ameghino's description is inadequate, and we have not been able to locate his types. Nevertheless, his statement that the molars are rooted, that the upper molars have no vertical grooves, and that the lower molars have a persistent fossette would preclude identity or close resemblance with *Ethegotherium,* and indeed that description suggests that *Eohegetotherium* is not a hegetotheriid.

ETHEGOTHERIUM CARETTEI (Minoprio, 1947), new combination

Figure 18 and Plate 5

Prohegetotherium carettei, Minoprio, 1947, p. 371; Simpson and Minoprio, 1949, p. 21.

Type: M.A.C.N. No. 16609. Skull and jaws.

Hypodigm: Type only.

Horizon and Locality: Type area of the Divisadero Largo formation, Mendoza, Argentina.

Diagnosis: Only known species of *Ethegotherium.*

Comments: We have no further material of this species, but Patterson has joined Minoprio in further study of the original on which the foregoing generic diagnosis has been based.

Notoungulata ?, indet.

M.A.C.N. No. 16610 is a fragment of a right lower jaw with poorly preserved P_3-M_2. It was at first identified as *Interatherium* sp. (Minoprio, 1947) and later as a probable interatheriid of indeterminate genus but not *Interatherium* (Simpson and Minoprio, 1949). Further study with better facilities now shows that this specimen definitely is not an interatheriid, but still does not permit identification. The teeth are brachydont and P_3-M_2 are all notably short and broad. P_{3-4} are submolariform but with talonids much smaller than trigonids. On M_2 the talonid is about as long as the trigonid and slightly narrower. These or other visible characters are insufficient for identification of the family or genus, but suggest that the animal is probably a rather peculiar notoungulate. The visible characters are distinct from those of any definitely identified mammal in the Divisadero Largo, and the presence of another genus (and, quite likely, family) is indicated.

Order and Family Uncertain

ACAMANA,[1] new genus

Type: Acamana ambiguus, below.

Known Distribution: Divisadero Largo formation, Mendoza, Argentina.

Definition: I^{1-2} transversely placed between anterior parts of opposite I^3s; section at alveoli elliptical with anteroposterior long axis. I^3 comparatively very large; circular in section at alveolus; with long, heavy, curving root ascending posterodorsally in facial process of premaxilla. Diastema posterior to I^3, followed by C of moderate size, more or less the size of I^2. Long diastema posterior to canine. Palatine processes of premaxillae small and short, with small, nonconfluent anterior palatine foramina at premaxilla-maxillary suture. Palatine processes of maxillae in canine-premolar region broad, deeply and smoothly arched dorsally.

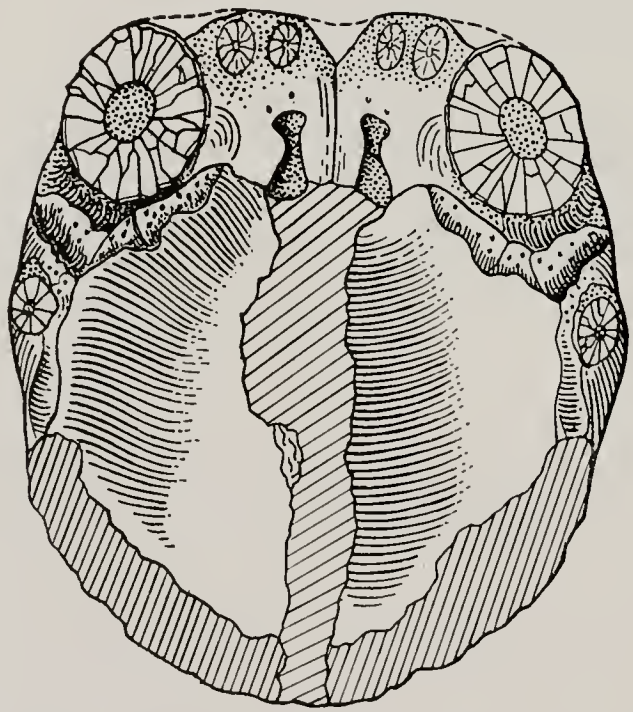

Fig. 19. *Acamana ambiguus.* M.H.N.M. No. 3010 P.V., type, part of rostrum. Palatal view, somewhat diagrammatic and with left side partly restored from right. X2/3.

1 Latinized from Aka-Manah, the name of a Persian demon. Again we follow the lead of Ameghino, who applied to a Patagonian fossil mammal the name *Asmodeus,* also a latinized version of the name of a Persian demon. It seems appropriate that so peculiar and, to a taxonomist, so annoying an animal should have a demoniac name. The name *Setebos* Roth, also applied to a Patagonian fossil mammal, is in the same spirit.

Affinities: As a precaution, the generic definition is based entirely on the most characteristic fragments and those certainly belonging to a single individual. Another possibly associated fragment is mentioned under the species, below, and adds somewhat to possible characters of the genus. The generic definition shows beyond any doubt that this is a very distinctive animal and one that should be readily recognizable if other specimens are found. So extraordinary an animal must be placed on record, and in spite of the inadequacy of the materials assignment of a name for purposes of discussion seems to us the lesser of two evils. This animal certainly does not belong to any genus in which the same parts are known. The possibility that the genus may have been known by, say, an isolated cheek tooth cannot be totally excluded but is remote.

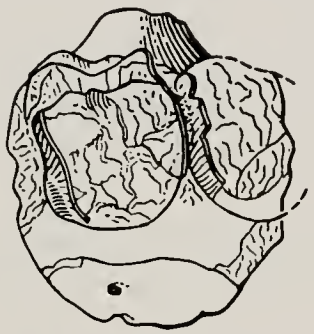

Fig. 20. *Acamana ambiguus.* M.H.N.M. No. 3011 P.V., perhaps same individual as type (M.H.N.M. No. 3010 P.V.), fragment of left maxilla with incomplete M^{2-3}. Crown view. X2/3.

Anything even approximating this arrangement of the anterior upper dentition is unknown in any previously described South American genus, family, or order. The presence of tusks followed by diastemata is superficially astrapothere-like, but the resemblance is distant and relationship is at once excluded by the fact that in astrapotheres the tusks are canines and in *Acamana* certainly incisors. The presence of somewhat tusklike or caniniform incisors does characterize the Leontiniidae, but that resemblance also seems superficial. In leontiniids the caniniform incisors are much less enlarged than in *Acamana* and are I^1 or I^2 in all known cases, not I^3 as in *Acamana.* Diastemata are small or, usually, completely absent in leontiniids, and there are decidedly more differences than resemblances throughout this region. It is perhaps conceivable that *Acamana* is on an

extremely aberrant lineage of common origin with the Leontiniidae, but one must judge relationships by resemblances, here extremely tenuous, and not by the mere possibility that the observed large differences might somehow have diverged from a common ancestry.

No other comparisons seem to have any significance, and we think it nearly certain that *Acamana* belongs to an otherwise unknown family, although we prefer to await broader knowledge of the characters of the group before going beyond the minimum nomenclatural requirement of genus and species. It is by no means impossible that *Acamana* represents a new order, but definite espousal of that hypothesis is not now warranted. We feel that *Acamana* is probably a placental ungulate, but even that is uncertain, and we can go no further at present.

Acamana ambiguus,[1] new species

Figures 19-20

Type: M.H.N.M. No. 3010 P.V., anterior part of palate and adjacent parts of face.

Hypodigm: Type only. Another fragment possibly of the same individual is mentioned below but is not now definitely included in the hypodigm.

Horizon and Locality: Divisadero Largo formation, bed G of section in stratigraphic part of this paper, Mendoza, Argentina.

Diagnosis: Only known species of *Acamana.*

Description: The principal fragments, constituting the type, are somewhat difficult to interpret but their characters must be close to those given in the definition and sketch reconstruction. I^{1-2} are evident on the right side only and even there I^1 is somewhat obscure but is probably about as shown. On the left side the alveolar margin posterior to I^3 was broken and the break has been polished to bring out what is preserved. Here the canine is represented only by a matrix-filled alveolus smaller at this section level than at the mouth as shown on the right side. Probably this indicates that the canine had a short and tapering root, rather than any great asymmetry on the two sides.

Perhaps belonging to the same individual or species is a fragment of the left maxilla with parts of M^{2-3}, M.H.N.M. No.

1 Latin, "uncertain" (as to affinities). As Aka-Manah is male in Persian demonology, we construe *Acamana* as masculine. There are numerous exceptions to the rule that Latin nouns ending in *-a* are feminine, e.g. *nauta,* "sailor."

3011 P.V. The basal contour of M^2 is rounded subquadrate, slightly wider than long, with a rather sharp groove medial, on the buccal margin, between the two buccal roots. The heavier, single lingual root is only flattened or very slightly grooved on the lingual face. Of the crown, only enough remains to show that it was brachydont and had a sharp, narrow anterolingual basal cingulum. The anterior part of M^3 has about the same size and contour as that of M^2. The possibly reduced posterior part is not preserved. The rather short anterior root for the zygomatic arch is above the posterior half of M^2 and anterior half of M^3.

No standard dimensions can be measured accurately. As an approximate indication of size, the width of the snout outside I^3 is roughly 10 cm. and the transverse diameter of the root of I^3 is about 2½ cm. M^2 of the maxillary fragment measured roughly 22 by 28 mm. This is much the largest mammal so far identified in this formation, although some of the unidentified scraps next to be mentioned are from one or more animals of loosely comparable size.

Unidentified Fragments

Numerous other, still more fragmentary specimens of fossil mammals have been collected. As we are unable to make useful identifications of these, their only present interest is the suggestion that the fauna is richer than the list of identified materials indicates. Some of these fragments have, nevertheless, been mentioned in previous publication. Among them are the specimens briefly described (as indeterminate) by Simpson and Minoprio (1949, pp. 23-24, fig. 10 [1]), some of which formed the basis for the mention by Minoprio (1951, p. 66) of "un nuevo género contemporáneo a *Astraponotus,*" i.e. a new genus of Mustersan age. We should make it explicit that no special taxonomic relationship to *Astraponotus* is established. It is indeed likely that a new genus is represented, but we cannot make a proper diagnosis or determine the relationships. There is some possibility that certain of the larger scraps belong to *Acamana,* but at present they are not useful in that connection. As discussed below, the age is now believed to be later than Mustersan.

1 In that figure the indicated orientation of the zygoma is incorrect. The view is lateroventral, the cavity shown in the upper middle part of the sketch is the glenoid fossa, and the anterior end is to the right.

STRATIGRAPHY

Our consideration of the stratigraphy of the Divisadero Largo formation depends mainly on an unpublished thesis by Olivo Chiotti and on extensive further observations by Minoprio (1951, 1958 and also hitherto unpublished data). Most of the other rather extensive published stratigraphic work on this general region refers primarily to earlier, especially Triassic, beds and has only background interest for the present subject. That literature has been reviewed by Romer (1960).

There have been much duplication and conflict of stratigraphic names in this region. The following summary sequence is now tentatively accepted.

Mogotes formation. No vertebrate fossils, but certainly late Cenozoic.

Higueral group. No vertebrate fossils in this region, but correlated with beds elsewhere containing late Tertiary mammals. Neogene.

"Areniscas entrecruzadas" or "inestratificadas." Have not been given a geographic formation name, and could be included in the Higueral, as by Minoprio (1958). No vertebrate fossils. Neogene.

Divisadero Largo formation. Mammalian fauna. Further discussed below.

Papagallos formation. No described fossils. Further discussed below.

Río Blanco or Victor formation. Some fossil plants. Triassic, possibly middle Triassic.

Cacheuta formation. A considerable vertebrate fauna, certainly Triassic, probably middle Triassic.[1]

(The thick pile of sediments below the Cacheuta, from Triassic down through the Paleozoic, does not concern us here.)

The Mogotes, Higueral and "Areniscas entrecruzadas" together form a great thickness of strata, over 3000 m. Disconformities within this part of the sequence appear to be local; no interruptions of regional significance have been noted by us or by others, and deposition appears to have been essentially

1 The Río Blanco or Victor, the Cacheuta, and the underlying Potrerillos and Las Cabras formations constitute what was long called the Rhaetic of Mendoza. Frenguelli (1944), who made important studies of these beds, referred them simply to the Triassic. Minoprio (1958) established the age of the Cacheuta more exactly as middle Triassic, perhaps just reaching the late Triassic. Romer (1960) also places the Cacheuta probably in the middle Triassic but considers early Triassic a possibility.

continuous. No fossils have been found in these beds in this area. In the Cacheuta basin, some 30 km. to the southwest, an almost precisely similar sequence occurs. There, near the base of the Mariño (= Higueral), some 20 m. above the highest repetition of "areniscas entrecruzadas" lithology, Patterson found a cranial region of a nothrotheriine sloth similar to *Pronothrotherium* but of rather more primitive aspect. This fortunate find suggests that deposition of the sequence went on throughout much of Pliocene time and perhaps began toward the end of the Miocene. In the same region but at a higher level, in the "tobas grises inferiores" which immediately overlie the Mariño, the type of *Typotheriopsis silveyrai* was found (Cabrera, 1937). That specimen suggests somewhat later Pliocene age, and still other, as yet mostly unpublished, specimens also tend to confirm the extension of this cycle of deposition through much of the late Tertiary.

A disconformity marks the Divisadero Largo — "Areniscas entrecruzadas" contact. Near the base of the latter occur two or three conglomerate beds composed of well-rounded, lustrous pebbles; similar conglomerates also occur at the base of the "Areniscas entrecruzadas" in the Cacheuta Basin. Below the Divisadero Largo in the type area there is a heavy, ridge-forming red sandstone and conglomerate. This has the field name of "Conglomerado rojo" in (unpublished) studies of government petroleum geologists and has been termed the "Horizonte Papagayense" by Rusconi (1950, p. 6). If recognized as a separate formation, the name "Papagallos formation" would apply and we tentatively so list it. The basal unit of the Divisadero Largo, as distinct from the tentative Papagallos, is Minoprio's bed J. In places it rests with apparent conformity on the Papagallos. This is especially the case at Arroyo Divisadero Largo, where bed J is a dark brown sandstone with occasional small geodes that differs on inspection only in color from the underlying Papagallos. Southward, toward the Arroyo Papagallos drainage, however, bed J contains an increasing number of pebbles and cobbles until it becomes a massive conglomerate that clearly reflects a major change in sedimentation. Subsurface data (as yet unpublished) suggest that a long period of erosion preceded the deposition of the Divisadero Largo. The Papagallos formation is almost inseparable from the Divisadero Largo formation in some exposures, its full extent has not been clearly established, and its age is unknown. Its recognition as

a formation is therefore provisional.[1] (In the accompanying map, Figure 21, it is included in the Divisadero Largo.)

The Papagallos is disconformable upon the Río Blanco, the contact being marked by a basal conglomerate and by clastic dikes that extend into the underlying sediments. No fossils have been described from it. The late Dr. Eduardo Carette is reported to have found some reptilian remains but these appear to have been lost. Search by us has been unproductive.

The very thick Triassic sediments appear to form a continuous sequence (Minoprio, 1958; Romer, 1960), despite rather abrupt changes in lithology between formations.

The Divisadero Largo outcrops in a band running from somewhat east of north to somewhat west of south about eight kilometers west of the city of Mendoza. (See map, Figure 21.) Good, fossiliferous exposures occur mainly in two areas, one the type locality on the east side of the Cerro Divisadero Largo (Plate 6), and the other about two kilometers south-southwest, near Papagallos (Plate 7). The beds dip in a general way westward, at Divisadero Largo generally somewhat north of west at angles of about 40°-50° and at Papagallos somewhat south of west at angles of about 20°-35°. These exposures are on the east limb of a broad, rather complex syncline, the other limb of which, more steeply tilted, is some five or six kilometers to the west in the vicinity of the Puesto Chambón. The western exposures include beds tentatively correlated with the Divisadero Largo by Chiotti and by Minoprio. The sequence is, however, complicated by faulting and no fossils have been found. Possible occurrence of the Divisadero Largo formation in the Cacheuta Basin lacks confirmation at present.

Between the localities Divisadero Largo and Papagallos the formation is continuous and without important differences in gross lithology. Relative levels can be reasonably established and guide levels traced through satisfactorily, but some individual beds are more local in character. The following section by Minoprio (1951) at Papagallos, here somewhat abbreviated,

1 The subsurface data at localities other than Divisadero Largo and Papagallos suggesting a significant disconformity between the Divisadero Largo formation and the Papagallos formation (that is, between the "estratos con anhidrita" and the "conglomerado rojo" of their nomenclature) have been obtained by geologists of the Yacimientos Petrolíferos Fiscales ("Y.P.F."). They have hitherto been working with the scheme here adopted, showing those two entities as distinct stratigraphic formations. At present, however, they are investigating the possibility that the Papagallos or "conglomerado rojo" is to be considered a basal facies in the Tertiary rather than a distinct formation, especially as regards its upper part. (Personal communication from Y.P.F. geologist Dr. Edgardo Rolleri to Minoprio, 24 March 1961.)

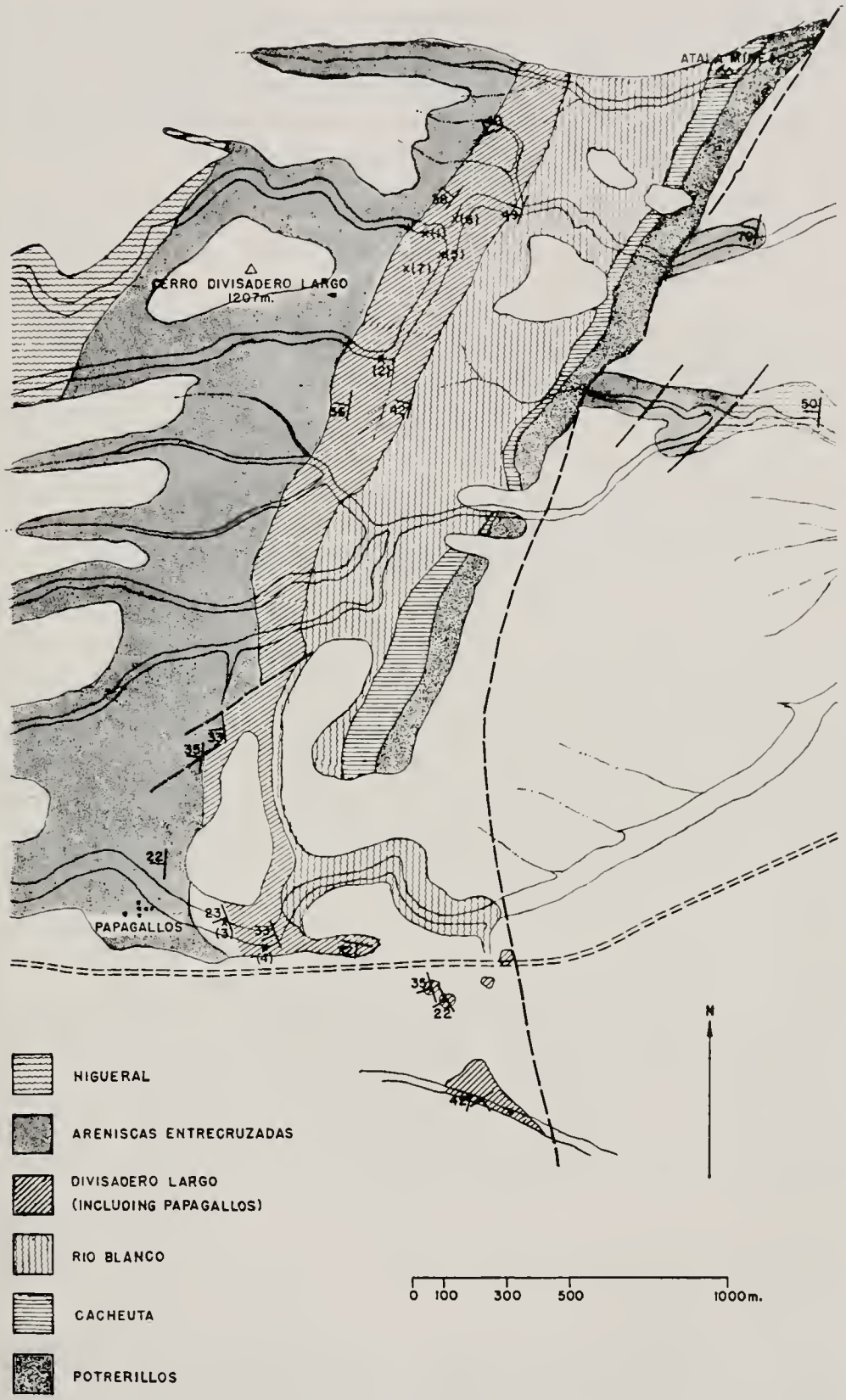

Fig. 21. Sketch map of the mammal-bearing exposures of the Divisadero Largo formation and of adjacent formations. Besides dip and strike symbols, some fossil localities are shown (X and number in parenthesis). (After Simpson and Minoprio, data from Chiotti with additions by Minoprio.)

is sufficiently characteristic of the whole fossiliferous area. The section has been checked and slightly modified by Patterson and, in a much more cursory way, by Simpson in the field.

A. Conglomerate, pebbles 2-4 cm. in gray sandstone matrix. 2 m. Base of "Areniscas entrecruzadas."

~~~~~~~~~~Top of Divisadero Largo formation~~~~~~~~~~

B-C. Thin-bedded clays, greenish above, reddish to violet below, with some sandstone. 100 m.

D. Dark chocolate-colored sandstones, "Upper chocolate cornice," a guide horizon. 3 m.

E. Pale or light purplish, finebedded marl. 3 m.

F. Chocolate, buff, or khaki fine sandstones, base harder and forming a lower "chocolate cornice." 42 m.

G. Lower pale chocolate, buff, or khaki fine sandstones. 65 m.

H-I. Darker chocolate fine-grained sandstones. 60 m.

J. Pale maroon conglomerate or puddingstone. 4 m.

~~~~~~~~~~Base of Divisadero Largo formation?~~~~~~~~~~

K-L. Fine, bright-red sandstones with basal conglomerate. 57½ m. Papagallos formation (but see note on p. 282).

Petroleum geologists of the Yacimientos Petrolíferos Fiscales ("Y.P.F.," the government oil organization) in their field notes have been referring to Minoprio's B-C as "areniscas abigarradas" and D-J as "estratos con anhidrita." Those two units, together, thus correspond with our (here slightly redefined) Divisadero Largo formation.

No determinate fossils have been found in A-E or J-L of Minoprio's Papagallos section or their lateral equivalents at Divisadero Largo or elsewhere. The known fauna is thus confined to F-I, hence to the lower and middle, not upper, parts of the Divisadero Largo formation and to the lower of the two Y.P.F. units.[1] Some surface finds had washed down from indeterminate levels and some fossils were collected without adequate stratigraphic information or with levels noted in ways we cannot reliably correlate with our subdivisions. We have, however, been able to make the following identification of fossils of known position in the sequence.

1 Patterson did find a fragment of an oldfieldthomasiid(?) mandible lying loose at the base of the "upper chocolate cornice," bed D. If the record could be relied on this would be the highest fossil yet found in the sequence, but unfortunately it cannot be. The formation is now much visited and chance discarding at any level of essentially worthless specimens by casual collectors is a definite possibility.

F. Crocodile. Turtle. *Groeberia minoprioi. Adiantoides leali. Brachystephanus postremus. Xenostephanus chiottii. Trachytherus? mendocensis. Ethegotherium carettei.*

G.-H. Crocodile. *Phoradiadius divortiensis. Brachystephanus postremus. Allalmeia atalaensis. Acamana ambiguus.*

I. Snake. Crocodile. *Brachystephanus postremus. Allalmeia atalaensis.*

CORRELATION

The mammalian faunal list as far as now definitely established and the possible bearing of the various forms on correlation are as follows:

Marsupialia

Groeberiidae

Groeberia minoprioi. Radically unlike anything known from elsewhere, to the familial level at least. Throws no light on correlation. One specimen described.

Litopterna

Proterotheriidae ?

Phoradiadius divortiensis. Generically sharply distinct from anything else known and only doubtfully referred to a known Riochican to Chapalmalalan family. Perhaps somewhat more like known Colhuehuapian-Santacrucian proterotheres, but the resemblance is not close enough to be of high value in correlation and markedly earlier age is not excluded. Moderately common but all specimens very fragmentary.

Adianthidae

Adiantoides leali. Generically well distinct but apparently allied to and more primitive than Colhuehuapian-Santacrucian *Adianthus.* More sharply distinct from Deseadan *Proadiantus* but apparently at a more or less comparable level of specialization. Hitherto known range of family Deseadan-Santacrucian. One specimen, associated skull and jaws.

Notoungulata

Oldfieldthomasiidae ?

Brachystephanus postremus, *Allalmeia atalaensis*, *Xenostephanus chiottii*: Very distinct genera referred with strong doubt to a family otherwise known from Riochican to Mustersan. These forms are primitive in aspect or in evolutionary level and might suggest approximately

Casamayoran age, but they are not phyletically near any known Casamayoran genera. *Brachystephanus* the commonest known fossil in the formation. *Xenostephanus* and *Allalmeia* moderately abundant. Some associated materials of each. There may be some other, now undefinable forms in this general group.

Mesotheriidae

Trachytherus? mendocensis. *Trachytherus* is otherwise known only from the Deseadan. This distinctive species probably does not belong to that genus although certainly allied to it. It is quite unlike anything known from the Mustersan or earlier. The degree of specialization could correspond with Deseadan or could be somewhat earlier but still post-Mustersan. Two specimens identified, both fragmentary.

Hegetotheriidae

Ethegotherium carettei. Allied to but more primitive than Colhuehuapian-Santacrucian *Hegetotherium*. Phyletically distinct from Deseadan *Prohegetotherium* but apparently at a roughly comparable evolutionary level. One known specimen, associated skull and jaws.

Order and Family Uncertain

Acamana ambiguus. Radically unlike anything else known and at present with no bearing at all on correlation. One surely identified specimen, fragments of skull.

The known forms fall into three categories as regards their possible bearing on correlation:

1. Suggestive, in degree of evolutionary advance and in closest known relatives, of distinctly post-Mustersan, perhaps approximately Deseadan, age: *Phoradiadius, Adiantoides, Trachytherus?, Ethegotherium.*

2. Suggestive of earlier, perhaps approximately Casamayoran, age: *Brachystephanus, Allalmeia, Xenostephanus.*

3. Throwing no light at present on age determination within the Cenozoic: *Groeberia, Acamana.*

The third group may — indeed, must — be ignored as regards correlation. The first and second groups are in apparent conflict and at once raise the question as to whether in fact all these fossils are of appreciably the same age. Among earlier identified and described specimens (all those published before the present paper), it happened that so far as they were of known level all from the higher subdivision F belonged to the

apparently more advanced group 1 and those from the lower subdivisions H and I to the apparently less advanced group 2. It was, therefore, a virtually forced preliminary conclusion that those specimens might represent distinct faunas of (at least) two different ages. That hypothesis was accordingly expressed by one of us (Minoprio, 1951). The now greatly augmented data, however, do not support that view and suggest that a single fauna, that is, one without geologically appreciable differences in age, is represented.

It is now definitely established that a variety of forms of group 2, the apparently more primitive animals that suggested greater age for subdivisions H-1, occurs at all fossiliferous levels in the formation. *Brachystephanus postremus,* the only really common species in these collections, is positively identified throughout, from F down to I. That is very strong, if not absolutely conclusive, evidence against appreciable lapse of time. Certainly it precludes any such span as Casamayoran-Deseadan, as those two stages in their typical developments have no mammalian genera and few subfamilies or families in common. "Advanced" *Phoradiadius,* as far as levels are positively known, is from G-H, and is there definitely associated with "primitive" forms. It is true that the other "advanced" forms of known level are so far known only from F, but they are only three in number and are represented by four specimens. Obviously a species known from one or two specimens cannot be distributed throughout a sequence through which it nevertheless originally lived, and the particular level at which it is known is largely or entirely a matter of chance. Although the data do not demand an additional factor, it is also possible that sampling bias (unrelated to geological age) has been introduced somewhere along the line: differences of original ecology, of depositional conditions, or of recent recovery. Such possibilities are suggested by the facts that among the fossils so far known the species in the upper beds are more varied but individually less abundant than those of the lower beds, that only the smaller species are so far definitely recorded in the lowest beds, and that associated skeletal material (of any vertebrate group) of known level is all from the lowest beds. (There are, nevertheless, associated skulls and lower jaws from high levels.) However, those differences in the present rather small collections may, of course, prove to be due to chance rather than to sampling biases.

The physical stratigraphic evidence, although in itself inconclusive, is also consistent with unity of age and tends to

strengthen that conclusion. There are probable small intraformational hiatuses, as in virtually any deposit of this thickness, but as the formation is now delimited — including all beds with identified mammals — there is no intraformational conglomerate and nothing that looks like an important or regional disconformity. The lithology is rather uniform, certainly not so varied as in itself to suggest any marked change in conditions or lapse of time. The thickness, even if maximum figures are taken, is not greater than for many continental formations known to be of appreciably the same geological age throughout.

We conclude that we are dealing with a fauna of a single geological age and shall further discuss its correlation on that basis.

Direct correlation of this extremely peculiar fauna is made virtually impossible by the fact that it has no species and almost certainly no genera in common with any other known fauna. One of its families (Groeberiidae) is certainly, another (an unnamed family for *Acamana*) probably, unknown elsewhere. Two family references (Proterotheriidae and Oldfieldthomasiidae) are quite dubious. The respective positively known ranges of those families are Riochican-Chapalmalalan (virtually the whole Cenozoic) and Riochican-Mustersan. The three most definitely identified families are Adianthidae (Deseadan-Santacrucian), Mesotheriidae (Deseadan-Pampean), and Hegetotheriidae (dubiously Mustersan, definitely Deseadan-Pampean). That is not much help, beyond the suggestive fact that none of the definitely identified families has hitherto been surely known before the Deseadan.

Correlation of this fauna must be based, in the main, on evolutionary level rather than on community of taxa, a notoriously inconclusive procedure but one that in this case does lead to a fairly exact conclusion. Although exceptions can occur, the general rule in such cases is that the age of a fauna is more closely indicated by its most advanced than by its more primitive members. Late survival of primitive groups is much more frequent, at least, than precocious appearance of advanced groups. Pertinent instances are already known in South American faunas. *Protheosodon* in the Deseadan of Patagonia is a condylarth, or perhaps a very condylarth-like litoptern, decidedly pre-Deseadan in evolutionary level (Loomis, 1914; Patterson, unpublished study). The Deseadan genus *Trimerostephanos* is a member of the predominantly Casamayoran family Isotemnidae, and

(regardless of family reference) is clearly a primitive form of pre-Deseadan aspect. Another isotemnid-like form and a condylarth, both Eocene in aspect, even survive in a certainly long post-Deseadan, approximately Friasian, fauna in Colombia (McKenna, 1956). In spite of the quite rapid evolutionary advance in most lineages and in general faunal characteristics from Casamayoran into Deseadan time, it is thus already known that some lineages did remain comparatively static. Discovery of additional examples should therefore not be unduly surprising, and that might be particularly likely in a fauna such as the Divisadero Largo that is outside the normal or usual paths of South American mammalian evolution as previously known.

Among the advanced forms in the Divisadero Largo, *Trachytherus? mendocensis* and *Ethegotherium carettei* have their closest known relatives in the Deseadan and seem to be on a comparable evolutionary level or possibly slightly more primitive. *Adiantoides leali* has its probably closest relative in the Santacrucian but is distinctly more primitive and more nearly on a level with its collateral relative *Proadiantus* of the Deseadan. *Phoradiadius* looks somewhat more like post-Deseadan than known Deseadan litopterns, but the apparent relationship is not close in either case and the comparable Deseadan litopterns are few and may not adequately represent the evolutionary levels of that time. As is evident from the degrees of confidence of family assignments, relationships of the advanced elements in the fauna with Deseadan forms seem to be distinctly closer than those of the primitive elements with pre-Deseadan groups. That agrees with and reinforces the conclusion that the latter are phylogenetic relicts.

It is thus highly probable that the fauna is approximately Deseadan in age. Later age seems quite improbable. Slightly earlier, but still decidedly post-Mustersan, age is by no means excluded. Survival of the primitive forms would be somewhat more probable at the earliest time assignment warranted by other evidence, which would be more or less immediately pre-Deseadan. Although negative evidence must be viewed with suspicion, especially in a fauna still so imperfectly known, it is just possible that the absence of rodents has a bearing here. Rodents were just beginning to appear in this part, at least, of South America in the Deseadan. A slightly pre-Deseadan fauna might also be expected to be pre-rodent. Absence of rodents may well be purely accidental, but small mammals are here well represented, and

all comparably varied Deseadan and post-Deseadan South American faunas with small mammals do include known rodents. Still more tenuous evidence that rodents were still absent is provided by *Groeberia,* most rodent-like known South American marsupial, which may have been occupying a niche later conquered by rodents. Even the survival of the rodent-sized ungulate herbivores might have been more likely in the absence of rodents.

The conclusion is that the age of the Divisadero Largo fauna is approximately early Deseadan or latest pre-Deseadan. As regards the latter possibility, it has long been realized from the evolutionary change in groups present in both Mustersan and Deseadan that a considerable time must have intervened. No mammalian faunas of intermediate age have been definitely identified, and at least one stage is here missing in the standard continental provincial sequence based on fossil mammals. The Divisadero Largo fauna may well belong in that gap, although if so, it probably belongs toward or at the end of the gap and does not fill the latter or divide it evenly. This cannot be made the basis for supplying a previously missing stage between Mustersan and Deseadan. In the first place, it is not certain that the Divisadero Largo does indeed belong there, and in the second place the known fauna is so scanty and what is known is so peculiar that it could not become a proper and useful standard for correlation.

GENERAL FAUNAL CHARACTERISTICS

The most striking peculiarity of this fauna is its taxonomic distinctness, already emphasized. Certainly all the species, probably all the genera, perhaps about a third of the families, and possibly even an order (for *Acamana*) are, on present knowledge, unique to this fauna. Moreover, most and perhaps all of these mammals do not seem to belong in or near lineages known from rich earlier and later faunas. The most likely exception is *Adiantoides,* which could conceivably be ancestral to *Adianthus,* but that is quite uncertain. With expectable sampling, ecological, and geographic differences, all other known South American mammalian faunas do fit reasonably well into a related continuum of faunal evolution. The Divisadero Largo fauna does not seem to be in or near that temporal mainstream but to be quite lateral to it. We do not know of any such markedly aberrant mammalian fauna from any other continent. Most suggestive, perhaps, is the Gashato fauna of Mongolia but there we

have no known Asiatic "mainstream" for comparison, and two of the genera (*Prodinoceras* and *Palaeostylops*) do tie in more or less closely with the North American sequence.

The evidence is that the Divisadero Largo fauna represents a sort of enclave, isolated in some way and probably peculiar in ecology. There is no evidence for geographic (or physiographic) isolation, and the isolating factors were probably themselves ecological. We are unable to propose any more definite hypothesis. The presence of turtles and crocodilians suggests only that there was surface water in the area and that the climate was at least warm temperate, but that is true of most "normal" South American Tertiary faunas, in many of which turtles and crocodilians are also fairly common elements, and in any case the Divisadero Largo sediments, like the majority of mammal-bearing beds everywhere, appear to be water-laid. The presence of a rather large snake is unusual but not unique, and the rarity of snakes in other South American Tertiary faunas is surely a matter of preservation rather than of the absence of those animals in the living faunas. The absence of carnivorous mammals in the known Divisadero Largo fauna is also certainly a matter of preservation and discovery and not an indicator of ecology. The fact that most of the known Divisadero Largo mammals (except *Acamana*) are small, both absolutely and in comparison with their nearest known relatives, may also be due to depositional conditions and chance or may possibly have some (quite unknown) ecological bearing.

Following Ameghino, *Pyrotherium* has long been considered the guide fossil for what is now called the Deseadan stage, and related genera are known from the earlier Casamayoran and Mustersan. The absence of pyrotheres from the Divisadero Largo fauna cannot, however, be considered particularly significant. Fairly well known local faunas certainly of Deseadan age but without *Pyrotherium* have already been reported (e.g. Chaffee, 1952). Leontiniids are in fact more constantly present in Deseadan faunas and more useful as guide fossils for that stage. Their absence in the Divisadero Largo, if not accidental, may again be ascribed to the manifest ecological peculiarity of this fauna. Deseadan pyrotheres are larger than any mammals yet known from the Divisadero Largo, and Deseadan leontiniids are also larger than any of the latter with the possible exception of *Acamana*.

REFERENCES CITED

Cabrera, Ángel

1937. Notas sobre el suborden "Typotheria." Notas Mus. La Plata, vol. 2, Paleont. no. 8, pp. 17-43.

Chaffee, Robert G.

1952. The Deseadan vertebrate fauna of the Scarritt Pocket, Patagonia. Bull. Amer. Mus. Nat. Hist., vol. 98, pp. 503-562.

Frenguelli, Joaquin

1944. La serie del llamado Rético en el oeste argentino. Gaea, vol. 8, pp. 156-309.

Loomis, Frederic Brewster

1914. The Deseado formation of Patagonia. Amherst, Massachusetts, Amherst College.

McKenna, Malcolm C.

1956. Survival of primitive notoungulates and condylarths into the Miocene of Colombia. Amer. Jour. Sci., vol. 254, pp. 736-743.

Minoprio, José Luis

1947. Fósiles de la formación del Divisadero Largo. An. Soc. Cien. Argentina, vol. 144, pp. 365-378.

1951. Nota previa sobre los pisos de la formación del Divisadero Largo (Mendoza). An. Soc. Cien. Argentina, vol. 152, pp. 63-67.

1958. Posición estratigráfica de los estegocéfalos de Mendoza y principales fósiles correlacionados en terrenos circunvecinos. Bol. Acad. Cien. Córdoba, vol. 40, pp. 293-319.

Palmer, T. S.

1904. Index generum mammalium. U.S. Dept. Agric., North American Fauna, no. 23.

Patterson, Bryan

1936. The internal structure of the ear in some notoungulates. Geol. Ser. Field Mus. Nat. Hist., vol. 6, pp. 199-227.

1940. An adianthine litoptern from the Deseado formation of Patagonia. Geol. Ser. Field Mus. Nat. Hist., vol. 8, pp. 13-20.

1952. Un nuevo y extraordinario marsupial Deseadiano. Rev. Mus. Munic. Cien. Nat. Trad. Mar del Plata, vol. 1, pp. 39-44.

Patterson, Bryan, and Jorge Lucas Kraglievich

1960. Sistemática y nomenclatura de las aves fororracoideas del Plioceno argentino. Pub. Mus. Munic. Cien. Nat. Trad. Mar del Plata, vol. 1, pp. 1-49.

Romer, Alfred Sherwood

1960. Vertebrate-bearing continental Triassic strata in Mendoza region, Argentina. Bull. Geol. Soc. Amer., vol. 71, pp. 1279-1294.

Rusconi, Carlos

1946a. Nuevo mamífero fósil de Mendoza. Bol. Paleont. Buenos Aires, no. 20, 2 pp. unnumbered.

1946b. Algunos mamíferos, reptiles, y aves del oligoceno de Mendoza. Rev. Soc. Hist. Geogr. de Cuyo (Mendoza), vol. 2, pp. 1-37.

1946c. Ave y reptil oligocenos de Mendoza. Bol. Paleont. Buenos Aires, no. 21, 3 pp. unnumbered.

1950. Presencia de laberintodontes en varias regiones de Mendoza. Rev. Mus. Hist. Nat. Mendoza, vol. 4, pp. 3-8.

SIMPSON, GEORGE GAYLORD

1936a. Structure of a primitive notoungulate cranium. Amer. Mus. Novitates, no. 824, pp. 1-31.

1936b. Skeletal remains and restoration of Eocene Entelonychia from Patagonia. Amer. Mus. Novitates, no. 826, pp. 1-12.

1945. The principles of classification and a classification of mammals. Bull. Amer. Mus. Nat. Hist., vol. 85, pp. i-xvi, 1-350.

SIMPSON, GEORGE GAYLORD, and JOSÉ LUIS MINOPRIO

1949. A new adianthine litoptern and associated mammals from a Deseadan faunule in Mendoza, Argentina. Amer. Mus. Novitates, no. 1434, pp. 1-27.

1950. Fauna del deseadense en Mendoza. An. Soc. Cien. Argentina, vol. 149, pp. 245-253. [An amended and abbreviated Spanish version of Simpson and Minoprio, 1949.]

PLATES

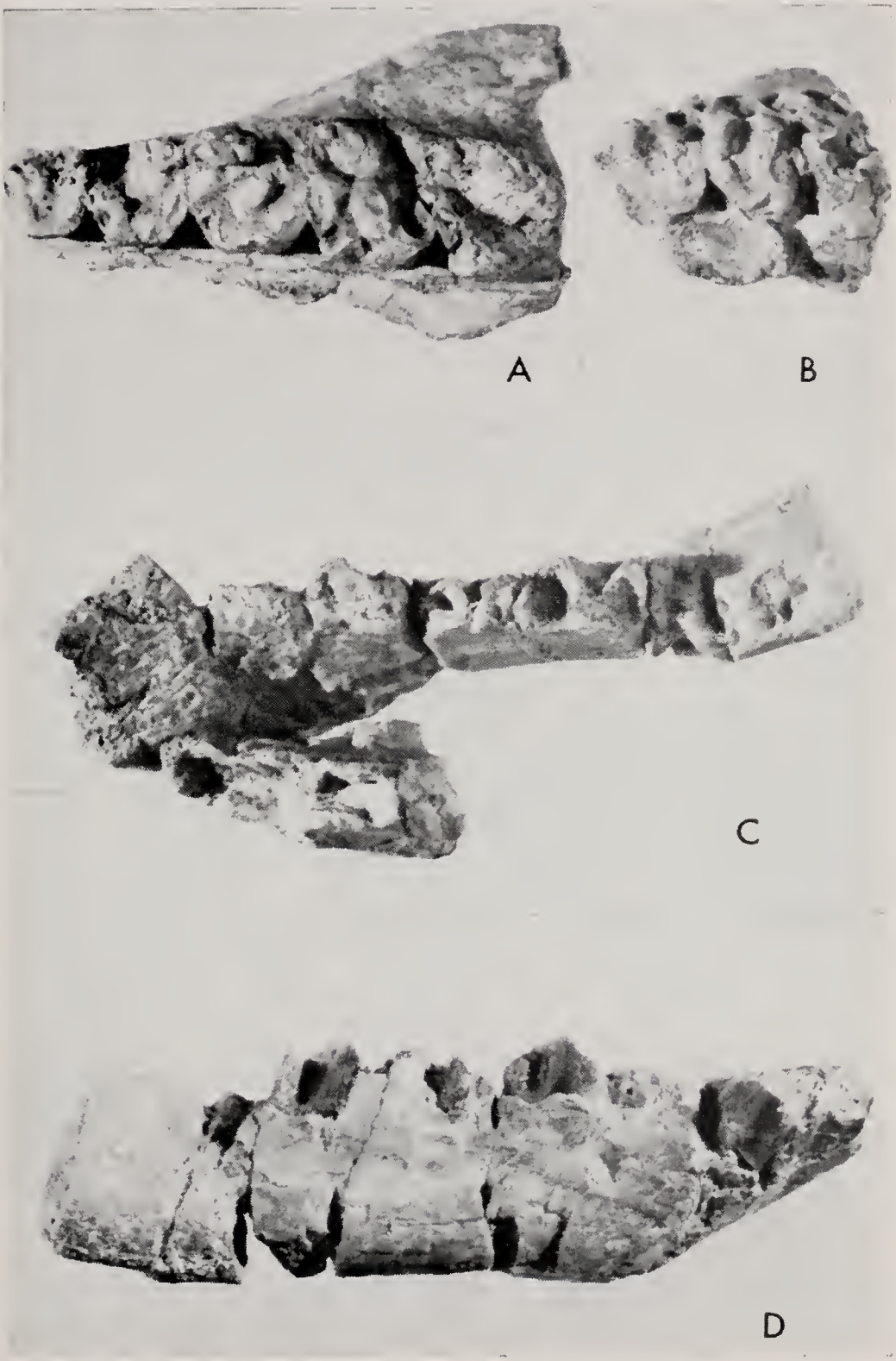

Plate 1. *Phoradiadius divortiensis*. *A*, A.M.N.H. No. 45930, left P^3-M^3. *B*, A.M.N.H. No. 45931, left dm^{3-4} and M^1. *C-D*, A.M.N.H. No. 45932, part of lower jaw with right P_{2-4} and fragments of other teeth. *C*, crown view. *D*, right lateral view. X1.5.

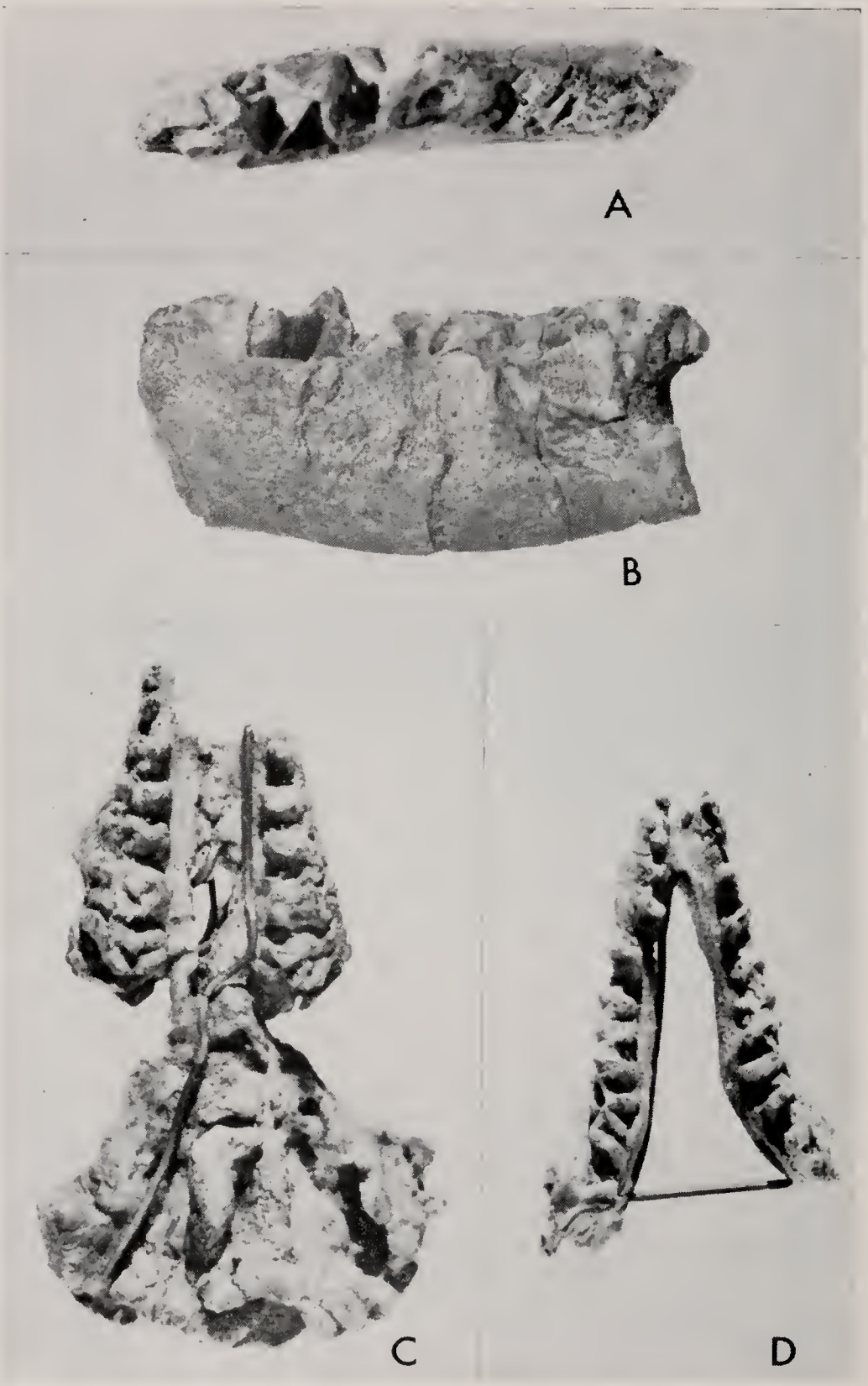

Plate 2. *A-B, Phoradiadius divortiensis.* A.M.N.H. No. 45933, part of right lower jaw with M_3. *A*, crown view. *B*, right lateral view. *C-D, Brachystephanus postremus.* A.M.N.H. No. 45945. *C*, skull, ventral view. *D*, lower jaw, dorsal view. X about 1.5.

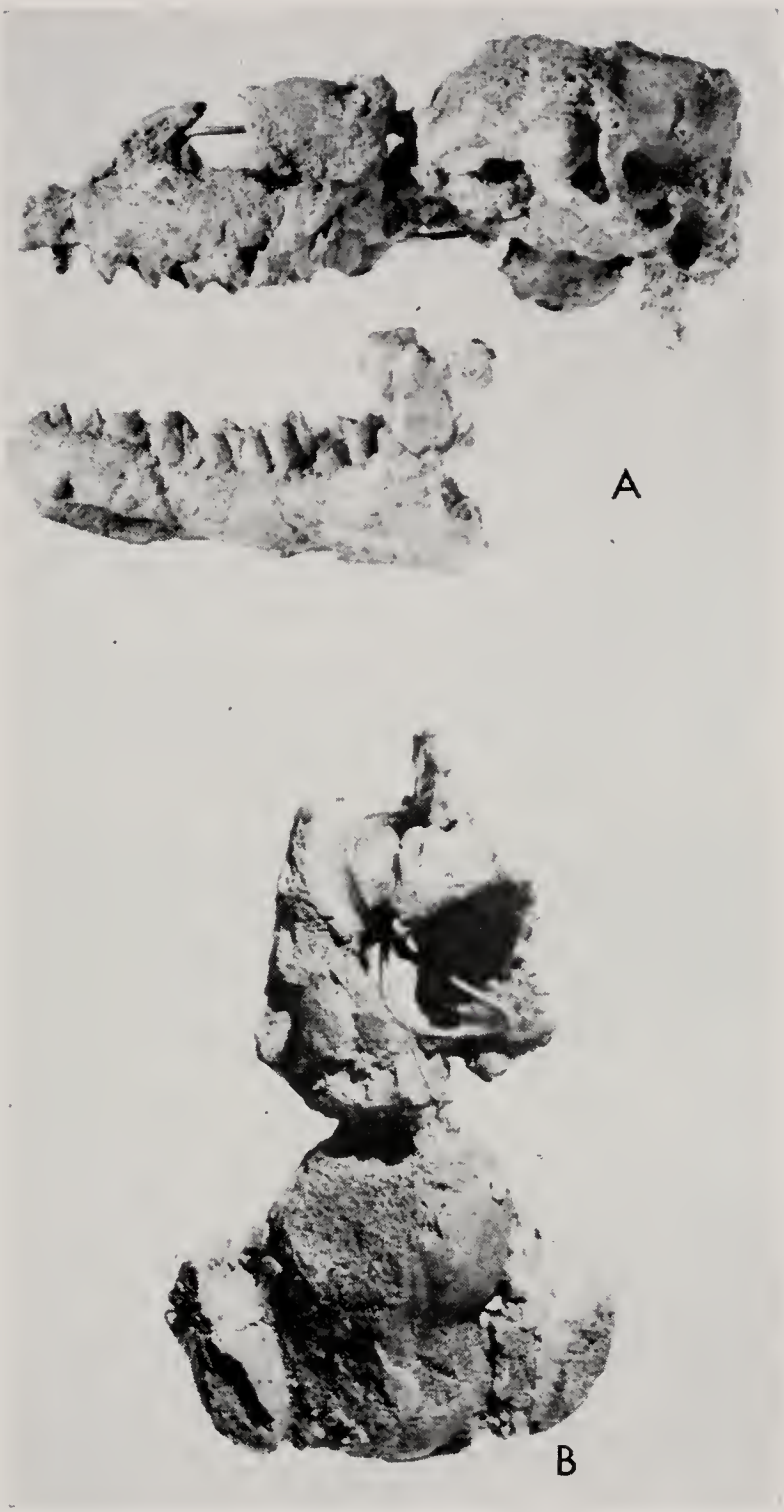

Plate 3. *Brachystephanus postremus*. A.M.N.H. No. 45945. *A*, partial skull and lower jaw, left lateral view. *B*, partial skull, dorsal view. X about 1.5.

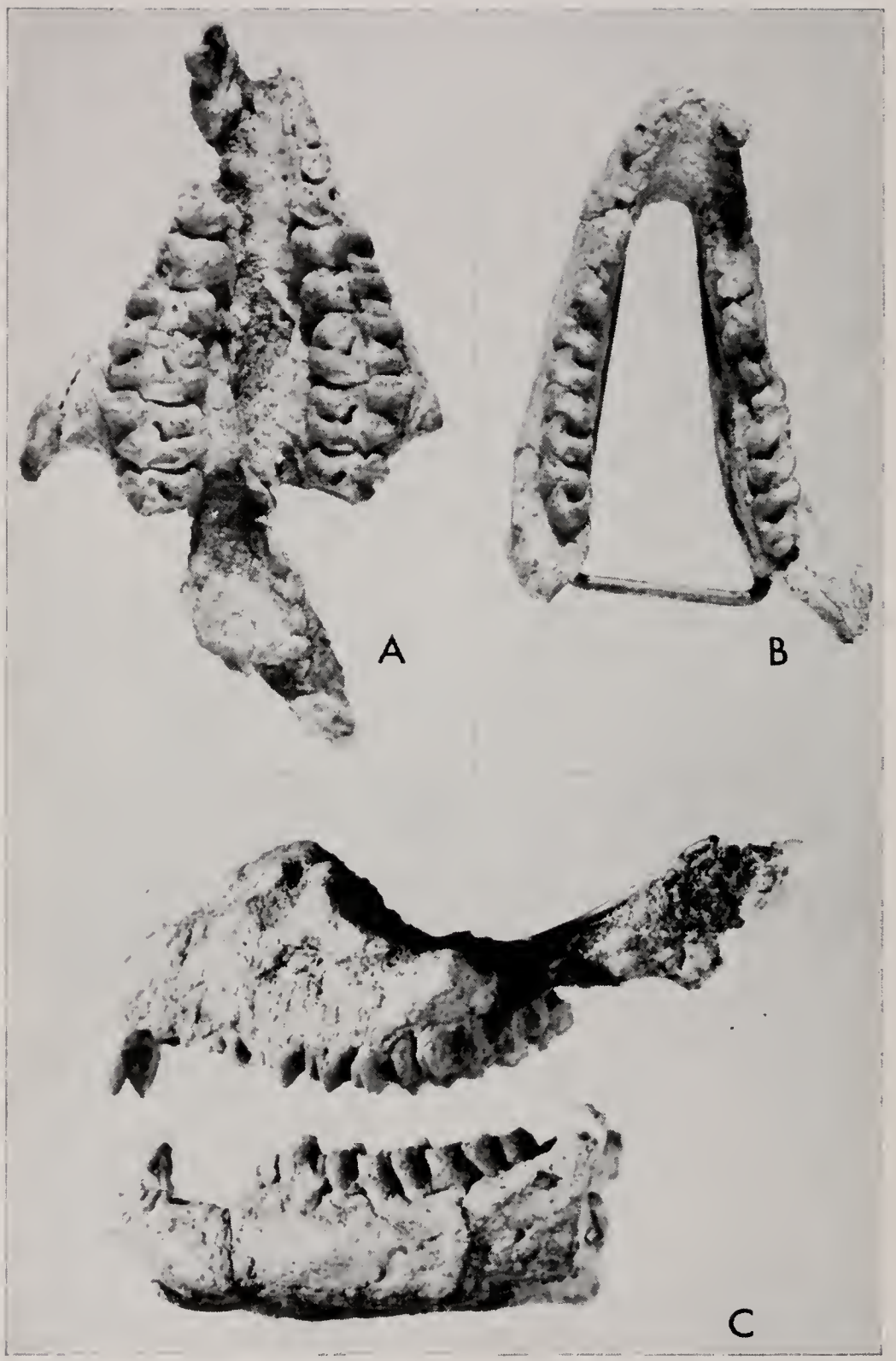

Plate 4. *Brachystephanus postremus.* Photographs of original of A.M. N.H. No. 45946, cast of type. *A*, incomplete skull, palatal view. *B*, incomplete lower jaw, dorsal view. *C*, incomplete skull and lower jaw, left lateral view. X about 1.5.

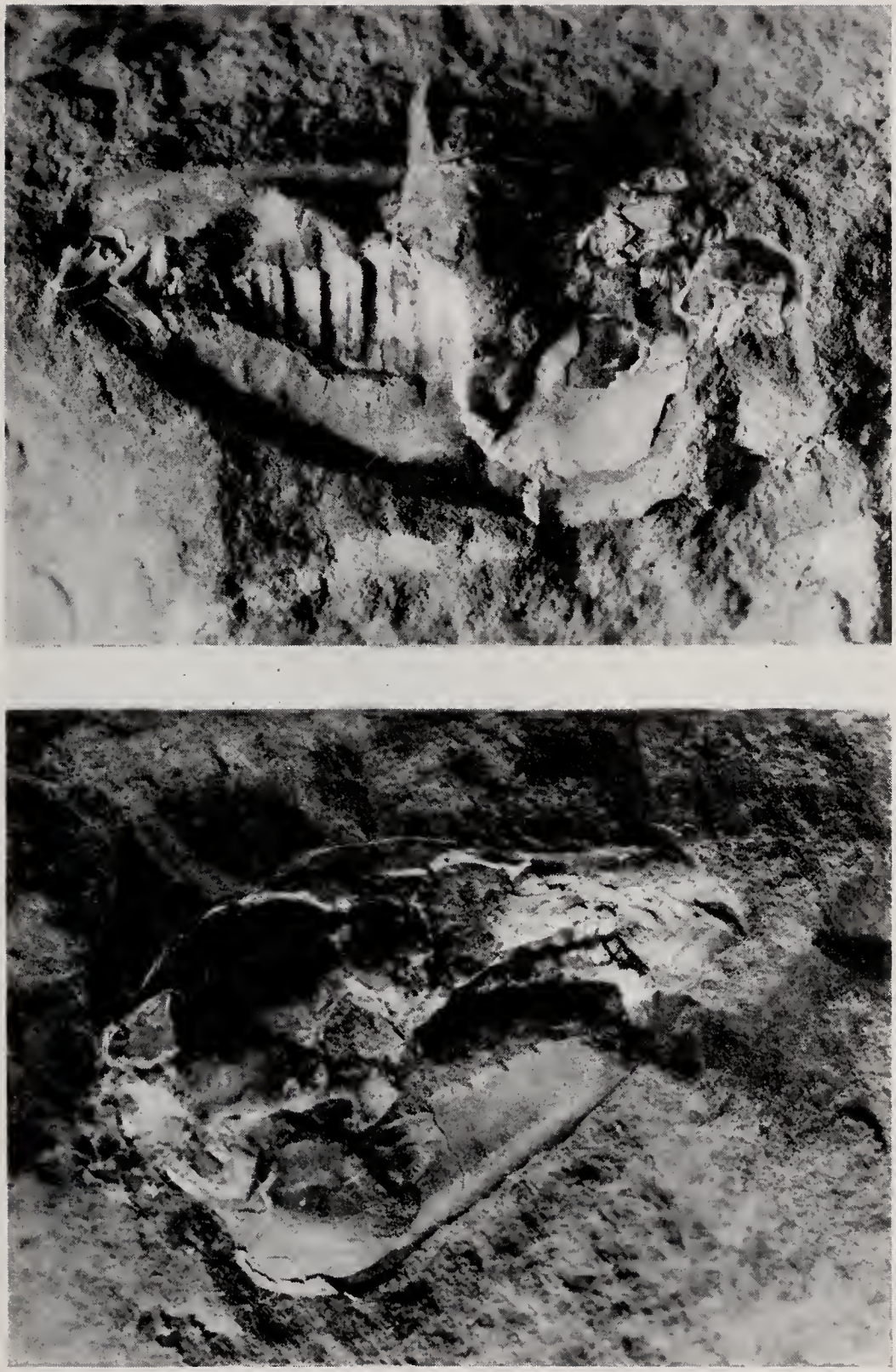

Plate 5. *Ethegotherium carettei.* M.A.C.N. No. 16609, type, skull and jaws. Split slab and counterpart. X1. (After Minoprio.)

Plate 6. Type section of the Divisadero Largo formation at east end of Cerro Divisadero Largo. The dip slope in the left background of the photograph is formed by the uppermost beds of the Papagallos formation (unit K of the section on p. 84) with some still adhering patches of the basal Divisadero Largo unit (bed J). Beds H and I are not visible. *A*, the basal conglomerates of the "areniscas entrecruzadas"; *B-C*, the banded "areniscas abigarradas," the upper part of the Divisadero Largo; *D*, the prominent "chocolate cornice"; *E*, the light purplish beds; *F* and *G*, fossiliferous units; *Q*, horizontally lying Quaternary. The bank in the left foreground follows very nearly the dip and strike of one level in *F*. Arrows indicate two of several fossil levels at this locality. (Photograph by Minoprio, after Simpson and Minoprio.)

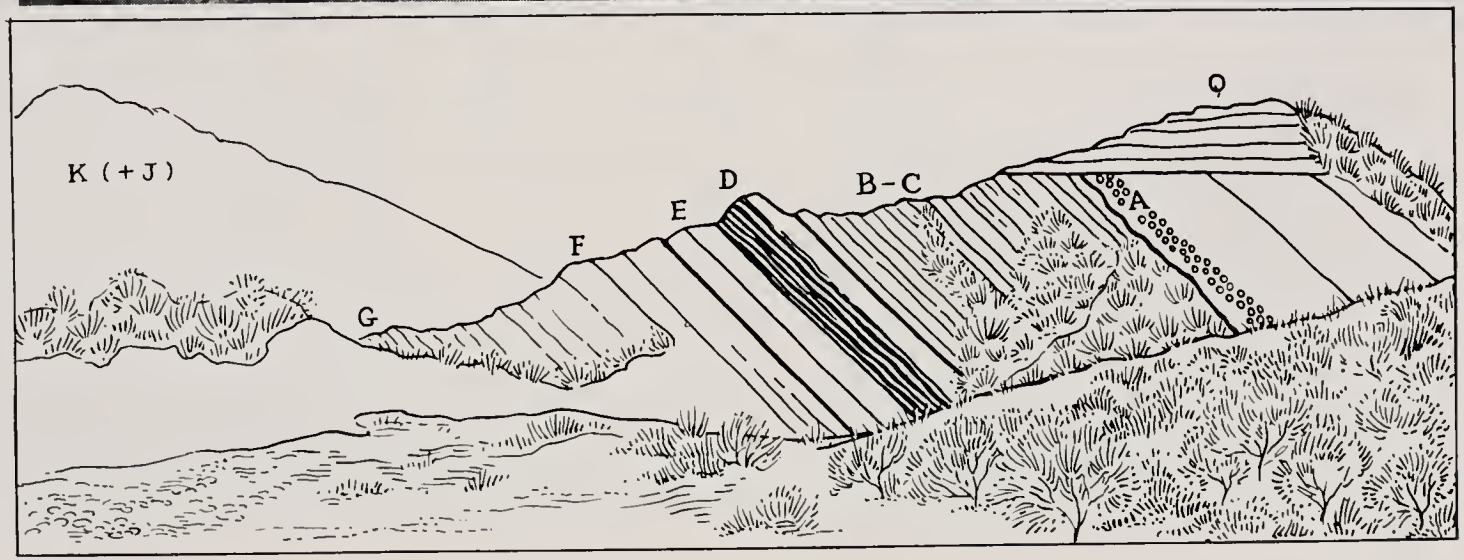
K (+J)
G
F
E
D
B-C
A
Q

Plate 7. The upper photograph shows a general view westward in the type area of the Divisadero Largo formation. The buildings in the center are at the Mina Atala, on the Cacheuta formation. The low pyramidal peak, upper left, is the Divisadero Largo, with horizontal Quaternary deposits forming the top of the peak. The type Divisadero Largo formation is on the lower slopes and in the arroyo below the peak. (Photograph by Minoprio.)

The lower photograph shows a general view westward in the vicinity of Papagallos. The buildings near the center are the Estancia Papagallos, on the "areniscas entrecruzadas." Fossiliferous exposures of the Divisadero Largo formation occur in the cut bank of the arroyo seen to the right and nearer than the estancia. (Photograph by Minoprio.)

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ON SOME BURMESE EARTHWORMS OF THE MONILIGASTRID GENUS *DRAWIDA*

BY G. E. GATES
University of Maine, Orono

CAMBRIDGE, MASS., U.S.A.
PRINTED FOR THE MUSEUM
JULY 23, 1962

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Johnsonia (quarto) 1941 — A publication of the Department of Mollusks. Vol. 4, no. 40 is current.

Occasional Papers of the Department of Mollusks (octavo) 1945 — Vol. 2, no. 28 is current.

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No. 5 — *On Some Burmese Earthworms of the Moniligastrid Genus* Drawida[1]

By G. E. Gates

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INTRODUCTION

This contribution completes publication of results of the author's study of Burmese moniligastrids. Specimens listed herein, with few exceptions, were collected between 1932 and the end of 1941 when the survey was finally terminated by the Japanese invasion. Locality lists for the period subsequent to 1932 probably are complete for most of the species considered below, though information about certain anatomical and other matters

[1] From a manuscript written during tenure of a John Simon Guggenheim Fellowship.

is available no longer. Some comparable data for one species was obtained recently, through assistance of Dr. H. K. Bhatti, from a Pakistani series. Unpublished records of other Burmese drawidas were destroyed along with the specimens during World War II.

The Burma survey provided, for the first time, considerable material of moniligastrid species. The variation, both individual and geographic, that was revealed required consideration (p. 308) of the usefulness to taxonomy of various characters. In addition to the taxonomic accounts, discussions of anatomy (pp. 299 and 305) provide the foundation for a first attempt at a phylogeny of the family (p. 355), as well as for discussion of certain assumptions basic in classical phylogenies. An "ingenious" contraction theory, the only previous attempt to bridge the gap between moniligastrids and other megadriles, is critically examined for the first time (p. 363), and other ways in which early oligochaete evolution may have proceeded are suggested.

SYSTEMATICS

Oligochaeta, Class or Order

The lower rank was acceptable to classical authorities, Beddard (1895), Michaelsen (1900, 1921, 1928-1930) and Stephenson (1923, 1930). The order, along with the Polychaeta, long was included in a class Chaetopoda. Since 1900, oligochaetes have been found to be more closely related to the leeches than to the polychaetes. Michaelsen's Acanthobdellidae, in Kükenthal and Krumbach's massive "Handbuch der Zoologie," is in the Oligochaeta and also in the Hirudinea! To show the relationship, some authorities, including Stephenson (1930), place the leeches also in the Chaetopoda. Michaelsen, however, erected for the two more closely related orders the class Clitellata which has not been generally accepted. *Acanthobdella* was retained in the Oligochaeta by Pickford (1948) and Yamaguchi (1953) but was excluded by Stephenson (1930) and Avel (1959). Though "The great gulf in intra-annelidan phylogeny is that which divides the polychaetes from the oligochaetes" Pickford (1948) believed that convenience required the three main annelidan groups to have equal rank as classes. If a classification is to indicate the closer leech-oligochaete relationship, some place presumably ought to be found for the Clitellata.

Between order and families, in his later systems Michaelsen interposed two (1921), then three (1928), and finally four (1930)

suborders as well as various series. These taxa were accepted by Pickford, Yamaguchi and Avel though with some modifications, including raising suborders (Pickford, Avel) to ordinal rank. This elaboration of the classification, in agreement with Stephenson (1930, p. 719), seems unwarranted by our present knowledge.

Pickford and Avel, as well as Stephenson, inadvertently reveal in their discussions a more immediate need for distinguishing two groups of oligochaetes. Three sets of terms have been used in the past: Terricolae and Limicolae, Megadrili and Microdrili, higher and lower oligochaetes. Many species obviously of earthworm size (sometimes as much as 12-18 mm. thick) and of terricolous habit formerly were considered to be microdrile or limicole. By 1930 Stephenson admitted it was sometimes convenient to include moniligastrids in the Megadrili. Later Yamaguchi (1953, p. 331) added the Haplotaxidae, Alluroididae and Syngenodrilidae. The terms indicative of size no longer are inappropriate though a very few microdriles may be somewhat larger than smallest megadriles. The Haplotaxidae, Alluroididae and Syngenodrilidae as well as the Moniligastridae, for more than thirty years, have been lumped together by the writer (*cf.* Gates, 1959) as "earthworms". No common word for "non-earthworms," however, has been available. Yamaguchi's division of the oligochaetes, which is in agreement with the author's practice, provides an appropriate pair of terms. The Megadrili, accordingly, includes the fourteen families of earthworms that are now recognized (Gates, 1959). The Microdrili comprises the remaining oligochaete families including the Acanthobdellidae. The megadrile group is the exact equivalent of Yamaguchi's Opisthopora diplotesticulata and of Michaelsen's Opisthopora. The latter was defined circuitously and, like other suborders and series, on vast extrapolations from very little data.

Megadrili and Microdrili, in the author's usage, are only convenient terms to facilitate communication. Accordingly, they require no formal definition or morphological characterization.

Family MONILIGASTRIDAE

This megadrile group has been conspicuous among classical families because of its homogeneity. Isolation from other oligochaetes was recognized early and the family could have been better defined as long ago as 1895 from information then available. Nevertheless, unique structure enabling recognition of isolation

has not yet been mentioned in a formal definition. Diagnostic characters are: intraseptal location of testes and male funnels, delimitation of an ovarian chamber from peri-esophageal and neural coelomic spaces, presence of enterosegmental organs, median union of last pair (or each of last two pairs) of hearts above the gut to open into dorsal trunk indirectly through a short vertical vessel. All of those characters were retained by the most aberrant individuals that have been found. In contrast to so much uniqueness, other megadrile families are defined by no single diagnostic character or by just one for a group (Megascolecidae) in which distinctive organs are lacking in parthenogenetic morphs.

A moniligastrid character, perhaps less likely to be unique, is provided by the prostomium. That organ, presumably as a result of considerable deepening and subsequent posterior extension of a slight transverse groove that once provided demarcation from the peristomium, is now attached to the roof of the buccal cavity behind level of intersegmental furrow 1/2. Still protrusible, and also capable of assuming a sucker-like shape, the moniligastrid prostomium at present appears not to be homologous with the longer and slenderer proboscis of certain glossoscolecids.

Absence of seminal vesicles is not confined to the Moniligastridae as those organs have disappeared in recent parthenogenetic morphs of several families. Extra-esophageal blood vessels are also lateral to the hearts in *Syngenodrilus* and may prove to be similarly located in other genera when long neglected vascular systems are studied. The single-layered clitellum, yolky ova, and location of male pores in front of the female apertures are all characters supposedly shared with the Alluroididae and Haplotaxidae as well as microdrile families.

Each portion of a moniligastrid septum containing a testis and male funnel has been called a testis sac. That characterization originally was given to, and in most megadriles still refers to, a truly coelomic space, containing one or both testes and male funnels of a segment, bounded by membranous or muscularized partitions, in communication with the exterior by an aperture in the funnel and the narrow gonoduct lumen as well as a minute male pore. Such a sac often is formed by development of partitions that seal off one (an unpaired sac) or two (paired sacs) ventral portions of the coelomic cavity. In various other megadriles the sac results from a series of gradual evolutionary changes such as approximation (or apparently so) of parietal

insertions of two consecutive septa, apposition of the septa peripherally finally followed occasionally by abortion of dorsal portions of the united septa. In all such cases the coelomic cavity of a particular segment is more or less markedly reduced but without affecting size of the metamere or diminishing total volume of coelomic space. Ocnerodrilid testis sacs are of a different sort. Each is merely a testis much enlarged by retention of developing gametes. The sac is a solid protuberance from the posterior face of the septum and may reach considerable size, even large enough to have been mistaken on various occasions for seminal vesicles. Any internal space (not artificially produced) that may appear is, of course, schizocoelic and not coelomic. The sac, unlike the seminal vesicles, is not in communication with the coelom nor does it open to the exterior. Sperm are released into the coelomic cavity by rupture of the sac wall and pass to the exterior via gonoducts that open to the interior and exterior as usual. The moniligastrid sac likewise is solid, any spaces not produced by preservation, fixation or dehydration, etc., in preparation for sectioning, again must be schizocoelic. Differences from the ocnerodrilid sac are two. First, the developing germ cells are proliferated, not posteriorly, but into the interior of a septum which becomes bulged anteriorly as well as posteriorly and more or less equally (if conditions permit) into two consecutive coelomic cavities. Second, the sac also contains a male funnel on which the testis sometimes even seems to be seated. Sperm no longer are released into the coelom to run the risk of ingestion by amoebocytes. Moniligastrid and ocnerodrilid testis sacs obviously are not homologous with any of the various kinds found in other megadriles.

The cavity of the moniligastrid ovarian chamber, unlike any schizocoelic spaces that may be present in otherwise solid testis sacs, is coelomic. The chamber, in more primitive forms, seems to be still bounded by the parietes peripherally but is closed off mesially from peri-esophageal and neural portions of the coelom that are omitted in figures purporting to show similarity to the testis sac. The chamber is closed off, in more advanced forms, from the parietes and then is arched like a horseshoe over the gut with one limb passing ventrally on each side. The ovarian segment is just as large as the one next behind, hence there is no reduction in size, merely a rearrangement of internal partitions. Complete closure of the chamber, rather curiously, does provide at maximal distension much more space for yolk and ova than had been available before.

Anatomy of the enterosegmental organs has been studied only in one species, *D. nepalensis* (cf. below). Function is unknown and the noncommittal name is intended only to indicate that they are metamerically repeated and are on the gut, into which each component may open at one or both ends.

The esophagus, in most megadriles studied by the author and also in South African acanthrodrilids (Pickford, 1937), ends in a narrow valve that must relax to allow passage of ingesta into the intestine. As moniligastrid gizzards long had been said to be at the beginning of the intestine, a valve was sought in front of the first gizzard but was not found. A narrowed portion of the gut much like a valve, concealed from view by deep saccu-lations of adjacent portions of the gut, eventually was located some distance behind the last gizzard. Thereafter, all of the gut between pharynx and the valve, regardless of length, was regarded as esophageal. The cuticular lining has been traced from the gizzards through several segments but not as yet all the way to the valve or to the buccal cavity. Determination of the segment of intestinal origin proved to be much more difficult than in other megadriles, partly because of close crowding of septa, partly because of delicacy of septa and of distended gut wall in material often not well preserved. Even in specimens carefully fixed in a relaxed condition, variation in location of the supposed valve was found. This perhaps should have been anticipated because of variation in gizzard location. The data secured from laboratory as well as field-preserved material were insufficient to show correlation between location of gizzard and valve. Situation of the supposed valve, in desmogasters and hastirogasters, as far back as the region xxv-xlii, suggested more careful examination of structure throughout the entire anterior portion of the gut. That, unfortunately, soon became impossible. However, if gizzards are at the beginning of the intestine, the esophagus has been extended in some lines of moniligastrid evolution from xii to xxv,[2] or through more segments than in bringing the gizzard of the supposed haplotaxid ancestor of the megadrili from v back into xii. There may then be no need for assuming disappearance of a more anterior gizzard and evolution of other, and perhaps intestinal, gizzards behind gonad segments.

Moniligastrid vasa deferentia, though often longer than in any other family, open at or close to the intersegmental furrow next behind the funnel septum. During their growth the male ducts

[2] An individual series of 2-12 moniligastrid gizzards may be anywhere in xii-xxx.

pass (always?) into the segment in front of the funnel septum. In certain circumstances the ducts conceivably could acquire external openings in that metamere so as to be in front of the testis septum. As an individual aberration (*Drawida* sp.) male pores sometimes are closer to the testis septum and so are in the position characterizing series Lumbriculina in Michaelsen's Prosopora. Situation of male pores does not now appear to be a proper character for defining suborders and their sections or series. One rather common and widely transported lumbricid even has the pores in front of the female apertures in agreement with the moniligastrids.

Moniligastrid prostates also are different from glands bearing that name in many megadriles. The structure appears to be more like that of the eudrilid euprostates except for presence on the coelomic face of a glandular tissue. Moniligastrid and eudrilid prostates usually have been said to be enlarged terminal portions of the male deferent apparatus which is correct only from the viewpoint of superficial appearance. Male gonoducts in the Oligochaeta (so far as is known) grow away from funnel rudiments and eventually to or through the parietes. Prostates, except in the Megascolecidae (where mesodermal origin is diagnostic), probably always are centripetal growths from the body wall. Proof of that origin, even in absence of information about developmental stages, is provided for the Eudrilidae as well as the Moniligastridae by occasional presence in adults of "prostates" that are not associated with male gonoducts.

Spermathecae of three moniligastrid genera, though monaxial, as in various microdrile and megadrile families, always are distinguished by location of the ampulla dorsally. Additionally, the duct always is longer than the distance between ampulla and spermathecal pore and often is much longer, a condition for which no explanation has been proffered. A secondary axis, when present (*Drawida* and *Moniligaster*), always lacks a special seminal chamber and so is different from the diverticulum of acanthodrilid, octochaetid and megascolecid spermathecae.

Most moniligastrid peculiarities were recognized in field-preserved material. As microscopic anatomy is studied in proper preservation, other typical characters are likely to be found, especially in the excretory system but perhaps also in the musculature. Formal expression of the uniqueness and isolation from other earthworms in more elaborate classifications would seem to require, as was recognized by Yamaguchi (1953), recognition of a taxon Moniligastrina.

Ovisacs, always dorsal, at maturity often extend back through several segments and are filled (in the many specimens that were examined by the author) not with ova but with granules of several sizes. These particles, long believed to be yolk, are of unknown chemical nature. After the breeding season the granules gradually disappear and the formerly distended sacs collapse. Massive production of yolk now appears to be another moniligastrid specialty.

The vascular system, in spite of some apparent generic differences with regard to the hearts, does conform strictly to a family pattern, as the last pair always is two segments in front of the ovarian metamere. Genital ducts, male and female, open to the exterior variously but always in conformity with the pattern. This means, in effect, that moniligastrid genera still are distinguishable, as in the past, only by location of the gonads. In contrast, the status of each genus similarly distinguished in other families now is suspect.

Rather large segment numbers now appear to be characteristic of the moniligastrids. The smallest desmogaster (86-115 by 4-5 mm.) has more than two hundred metameres, and the smallest drawida (30-41 by 1.5 mm.) has more than a hundred.

Habitats. Moniligastrids were believed (cf. Stephenson, 1930, p. 608) to need "moister conditions than any other family of earthworms, taken as a whole," presumably because of lack of dorsal pores — "usually connected with an aquatic habitat." The moisture requirement was deduced from casual site records and absence of species in the drier regions of India. Dorsal pores are indeed lacking in the limicoline Criodrilidae and Sparganophilidae but also are absent in the Hormogastridae as well as two large families, the Eudrilidae and Glossoscolecidae, that are mainly if not entirely terricolous. Almost any sort of earthworm is likely to be found at supposedly typical drawida sites, mud, under stones in water, in saturated soil by a spring, etc., during periods of drought. One introduced drawida now is established at Lahore where precipitation is less than twenty inches a year. In the dry zone of central Burma drawidas are common but the war prevented publication of data as to habitats. Burmese desmogasters certainly are not limicolous and probably most drawidas also are terricolous.

Distribution. India to Korea on the Asiatic mainland, Japan, Borneo, Sumatra. Absence of endemic species in the Philippines, Java and other Malaysian islands, even the Andamans, should

not be assumed until earthworms have been collected more systematically in those areas.

The range, with the exception of Sumatra, is the same as of the best known genus, *Drawida*. Ranges of other genera are much smaller and except for that of the South Indian *Moniligaster* apparently with internal discontinuities. However, few more than a hundred specimens (even if as many as that) of *Eupolygaster, Desmogaster* and *Hastirogaster* have been studied.

The distributions provide little support for the classical belief that *Drawida* is the youngest genus, or for its descent from *Moniligaster*.

Genus Drawida Michaelsen 1900

Sites of the testes, in the smallest juveniles that have been examined, were indicated by opacities in septum 9/10 near to or about at the usual ventral position of oligochaete gonads, i.e., near parietes and mesially. The septal thickening is larger in longer juveniles and higher up in the body. At maturity, the sac now markedly protuberant from the septum, usually is just above the gut.

Although the male pore is only one segment behind the testis septum, the vas deferens always is much longer than the distance between gonad and aperture, occasionally a hundred times or more longer. The gonoduct, as it leaves the male funnel, often passes downward for a short distance in a schizocoelic intraseptal space but apparently always emerges into the coelomic cavity of the preseptal segment where it is farther away from the site of its future opening to the exterior. Within that anterior metamere continued growth seems, judging from adult conditions, to have been random, looping the duct back and forth, up and down, even around the heart. Eventually, the duct passes back through the gonad septum and always enters the prostate of its own side. Before attaining that junction in some species, the duct penetrates into the body wall where it may join the prostate or turn back into the coelomic cavity. As the duct always reaches its proper gland, regardless of presence of similar glands nearby, a later portion at least of its growth seems no longer to have been aimless but directed. Control presumably is provided by some sort of attraction emanating from the prostate. If that influence is exercised while prostatic anlage are confined to the parietes, junction may take place there, after which some prostates, by their own further growth, carry an ectal

portion of the gonoduct back into the coelomic cavity again. Junction with other prostates appears to be acquired only after gonoducts and glands had emerged independently into the coelom. In such cases, attraction presumably still emanated from growing ental portions of the anlage which had gotten into the coelom before gonoducts had acquired junction. Unexplained, however, is the apparently invariable passage of gonoducts from the funnel septum into the anterior segment where they are farther away from the level at which they will finally open to the exterior. Return of the gonoduct to the postseptal metamere, on the contrary, could be attributable to prostatic attraction. Whether the gonoduct reaches its greatest elongation in the coelomic cavity of x before or after junction with the prostate cannot now be stated.

The prostates, according to early accounts, have at least three layers, a middle muscular one, an inner glandular, and an outer glandular, the latter derived either from the inner layer or from the peritoneum. Origin of the inner glandular layer was not mentioned but doubtless is ectodermal. The middle layer of moniligastrid prostates, at least in early growth stages, may well be muscular but in adults of various drawidas is often thin, translucent or transparent, sometimes reddish and brittle. The color, as in the clitellum, may have been "developed" after preservation but the peculiar texture seems "unlikely to have resulted from a post-mortem modification of muscle tissue. Whether muscular or otherwise, the middle layer gives to the prostates a wide variety of shapes, one of which seems to be characteristic in each species. The outer glandular layer completely covers the coelomic face of the capsule in some species, but in others is more restricted to an ental portion or to some rather definite zone or area.

Digitiform prostates, present in some species of each genus except *Moniligaster*, have been thought to be primitive. GM glands of one drawida, identical in structure with the supposedly primitive prostates except for the blind ental ending, were thought to show descent of the bitesticulate *Drawida* from the quadritesticulate *Desmogaster*. The latter genus has testes in septa 10/11-11/12 but extra prostates in the supposedly derived *Drawida* were so placed that testes would have been in septa 8/9-9/10. More recently, prostate-like glands were found (in other species) in segments vii-ix as well as in x where, alongside the real prostates, they are supernumerary. An extra gland

in x, closed entally just like the glands in vii-ix, obviously cannot be "the thickened terminal part" of a male gonoduct. Such an appearance, however, can be achieved if gonoducts during their centrifugal growth penetrate into apices of developing capsular glands.

The "prostates" in some species of *Drawida* (and also of *Desmogaster*) have no glandular investment but whether these "muscular" glands(?) are capsules that have lost the outer glandular layer is unknown.

Spermathecae of some drawidas are monaxial but ducts are slightly widened within the parietes. A similar thickening presumably was the rudiment from which a secondary axis was developed in various lines. This still reaches, in an early stage of evolution, only a little above the body wall but now is joined on one side by the slender spermathecal duct. A more obvious secondary axis, as well as an ectal portion of the male terminalia in various microdriles, long has been called an atrium. Spermathecal atria are thin-walled organs that may be digitiform or saccular and much longer or thicker than the main axis, or even thick-walled chambers that sometimes become bifid. Each atrial bifurcation, in a species group not otherwise presently distinguishable from *Drawida,* bears a dichotomously branched outgrowth that presumably is glandular. The atrial aperture of other species, in a distinctly demarcated genital marking, has been withdrawn into a preatrial (!) parietal invagination. Sperm rarely have been found in the atria and then only in an ectal portion. Function of the spermathecal atria is unknown but is unlikely to be the same as that of spermathecal diverticula in other megadriles which have a more or less distinctly demarcated seminal chamber solely for storage of the sperm received in copulation.

Ovaries of all drawidas always are in segment xi (abnormality excluded). This character, uniquely diagnostic among earthworms, greatly puzzled classical oligochaetologists, and has further consideration in a subsequent section.

Distribution. The natural range, as already noted, is that of the family, with exclusion of Sumatra, and is much larger than that of the supposedly all conquering megascolecid *Pheretima.* Transportation, presumably by man, has resulted in the following additions to the natural range: Aru, Soemba, Caroline Islands, Bahamas, and Puerto Rico.

Taxonomic Characters

The latest key to species of *Drawida* (Stephenson, 1923, pp. 127-130) has 48 couplets or triplets for 42 of the 43 species then known. Even so, all data except that in the original description was disregarded in entering *D. ghatensis* Michaelsen 1910. Many other species, it is now clear, would have been equally refractory if specimens additional to very short series or the unique type had been dissected. Brevity of early descriptions (often still unsupplemented) and immaturity (usually unrecognized) of types, in which definitive genital structure was incompletely developed or even undifferentiated, added to the difficulties.

Several classical characters, such as shape and position of testis sacs, shape of prostates (except when muscular), latitudinal location of female pores, presence or absence of dorsal pores, now are known to have no taxonomic validity. Relative widths of intersetal intervals, as Stephenson admitted, may differ from one part of the body to another as well as from one worm to another and also may vary according to degree of contraction or relaxation at preservation. Other characters are of little use because of limitation to presence or absence, as in the case of pigment and peripheral closure of ovarian chamber, or because condition of material often does not allow a decision as to which of those pairs is involved. The taxonomic value of characters provided by gizzards (number, location) and genital markings (number, location, shape, size), even after accumulation of considerable data, still remains to be determined.

Shape of muscular prostates, latitudinal location of spermathecal and male pores, as well as atrial characters, do have some, more or less limited use. Spermathecal pores may be at *B*, m*BC* or *C* but in Burmese worms are, with one exception, at the lateral level. Male pores may be at *B* (one Burmese species) or between *B* and m*BC* where differences are too small and variable to be useful. Spermathecal atria may be subject to considerable intraspecific modification. Thus, a slight symmetrical thickening of an ectal portion of the spermathecal duct has become, in the northern part of the *caerulea* range, a muscular diverticulum that is larger than the original axis. Great intraspecific variation in length of digitiform atria has been found in two of the better known species. Thin-walled saccular atria, on the contrary, are of about the same shape and size in a number of species.

The characters allowed to have taxonomic value by classical authorities, as Stephenson's key proves, were too few to enable recognition of relationships. Other characters now appear to be of greater significance. Length of male gonoducts may be distinctive in some species but confirmation is required as great intraspecific variation has been found in two of the better known forms. Entrance of male gonoducts into parietes prior to junction with prostates, emergence into the coelom before joining, intraparietal junctions that are concealed or obvious, now appear to be specifically invariable, but ducts of all Burmese species enter prostates directly, i.e., in the coelom without first passing into body wall. Shape of capsule in glandular prostates seems to be free of intraspecific variation but in many Burmese species is digitiform. More ectal portions of the deferent apparatus can provide a number of characters. Male pores in an apparently primitive stage are superficial, minute and recognizable with difficulty due to absence of differentiated structure around them. Often, areas containing the pores are protrusible in more or less characteristic shapes. Such porophores in a retracted state, and especially when delimited by deep grooves, have a rather discoidal appearance. Differences between states of complete protrusion and retraction, when unrecognized as such, have been thought to distinguish species (cf. synonymy of *nepalensis*). Adequate characterization still is impossible for some Burmese forms, in spite of examination of numerous specimens, because one or the other of the states has not been seen. Primary male pores may be invaginate and then the larger superficial apertures provide another character. Existence of parietal invaginations is suspected in certain species. In others a short ectal portion of the prostatic duct may prove to be eversible as a sort of penis. Deeper invaginations that were ignored or undetected by earlier authors also furnish important characters; penial bodies, tubular penes, genital markings and even glands may be present in chambers that reach into the coelomic cavities. Determination of relationships between muscular prostates and the coelomic copulatory chambers, as for instance in *D. caerulea*, may provide further characters.

An ectal portion of the spermathecae may repay more careful examination than it usually has had in the past. The primary spermathecal pore of one Burmese species is invaginated and the shallow parietal chamber contains a distinctly delimited genital marking.

Glands associated with epidermal genital markings provide a set of characters in addition to absence. Tubular glands, once thought to be prostates, have obvious though minute pores that were thought to be male pores. Size, relative to that of the real prostates, may be specifically distinctive. Solid glands have no lumen and presumably no aperture. The wall may be transparent to translucent or opaque and then is soft or tough. Shape and size, especially of the tough-walled glands, may vary in a single specimen but the condition of the outer layer now appears to be uniform within a species. Clear glands (with transparent walls) apparently do not become as large as the others and may be buried so deeply in the parietes as to be unrecognizable from the coelom without removal of most or all of the longitudinal musculature.

The excretory system, as in other supposedly holonephridial families, has had very little attention. Early ontogenetic abortion of nephridia in segment ii may prove to be common if not universal in the family. Later disappearance of organs in one or more segments of the genital region now seems likely to provide a set of taxonomically useful characters. Nephridia are vesiculate and the bladder is a diverticulum (or caecum) given off from the tubule shortly before entering the parietes in the few moniligastrids for which information has been recorded. Caecal bladders may prove to be characteristic of the family. Parietal portions of nephridial ducts now seem more likely to be of interest to systematists. Ducts enter the body wall near the ventral setae of postgenital segments in several species of *Desmogaster* and *Hastirogaster*. Entry, in anterior segments of a Japanese drawida, now is near the lateral setae though still at the lower level in postgenital segments. In two Burmese drawidas, for which information still is available, the parietes is entered, in postgonadal segments, at the lateral level. Within the body wall ducts may or may not pass directly to an epidermal aperture. In the latter case ducts grow ventrally or dorsally for some distance before finally turning towards the epidermis. Irregular alternation of nephropores between two or even three levels, usually with more or less asymmetry, has been found in several species. Nephropore locations, accordingly, need not indicate levels at which ducts enter the body wall.

Number of segments in types usually has been recorded. One type, 47 by 1.75 mm., has 150 segments. Another, 55 by 2 mm., has 165. The only record of less than a hundred segments (98)

is of a unique specimen that may be a posterior amputee. One Indian species was said to have more than 500 segments and five others have more than 300 or 400. Information available as to segments of *nepalensis* (129-180), *gracilis* (140-340) and other species does not suggest hatching with a definitive number. Much tedious counting doubtless will be required to determine specific limitations.

Color characterizations of the past often are of little or no importance to the taxonomist today. An unpigmented lumbricid species, *Octolasium cyaneum* (Savigny, 1826), by its name provides one bit of supporting evidence. Another lumbricid example is furnished by *Eisensia rosea* (Savigny, 1826) which usually appears to be unpigmented though minute yellowish or brownish (epidermal?) flecks often are recognizable under the binocular in older individuals. Colors sometimes mentioned, or occasionally shown in plates, are attributable to cuticular iridescence, blood, even to ingesta within the intestine or (especially at posterior end of the body) to accumulations of coelomic corpuscles and debris. A green color, apparently characteristic of a few species, cannot be traced to discrete particles. A beautiful red color of the clitellum in many drawidas is "developed" after preservation by formalin and perhaps also by other substances. The fine granules responsible for that color are in the outermost portion of the epidermal cells. Similarly located granules may be responsible for a striking orange or red coloration of the clitellum in live specimens of *E. rosea* but after preservation the pigment flecks appear to be yellowish or brownish.

Pigment usually is in or is associated with the circular muscle layer of the body wall but may extend into the longitudinal layer at the anterior end and dorsally. Presence of granules that appear to be red or reddish brown in sections through the body wall does not always confer a similar color. Such worms often seem to be blue, sometimes even a quite dark blue or almost black. The clitellar region, at maturity, of pigmented drawidas after preservation may be white though pigment is present underneath the epidermis.

A clitellum rarely has been recognized *in vivo* and moniligastrids were for a time placed in a group called Aclitelliens. The tumescence that has sometimes been noted in preserved specimens may have been developed by the preservatives. Except as interrupted by genital markings, the clitellum probably

is always annular in the Moniligastridae. Though intergeneric differences have been recognized they do not now appear to be of taxonomic importance.

Certain characters not mentioned in the taxonomic section as they now appear to be universal throughout the family are: absence of typhlosoles, supra-intestinal and calciferous glands; location of extra-esophageal blood vessels lateral to the hearts; presence of a subneural trunk that is adherent to the parietes rather than to the nerve cord as in the Lumbricidae. Seminal vesicles, possibly present in some ancestral form before direction of proliferation by the testes was reversed, always are absent. Penial and copulatory setae never have been found.

Drawida beddardi (Rosa)

1890. *Moniligaster beddardii* Rosa, Ann. Mus. Sto. Nat. Genova, 29:379. (Type locality, Chiala, Burma. No types.)
1894. *Moniligaster beddardi*, Bourne, Quart. Jour. Micros. Sci., 36:374.
1895. *Moniligaster barwelli* (part), Beddard, A Monograph of the Order of Oligochaeta, p. 200.
1900. *Drawida barwelli* (part), Michaelsen, Das Tierreich, 10:116.
1923. *Drawida barwelli* (part), Stephenson, (The Fauna of British India), Oligochaeta, p. 133.
1924. *Drawida barwelli* var. *hehoensis* + *D. "fluvaitilis"* Stephenson, Rec. Indian Mus., 26:324, 325. (Type localities, Heho plain and White Crow Stream, both near Yaungwhe. Types in the Indian Mus.)
1926. *Drawida teeta* Gates, *Idem*, 28:148. (Type locality, Yaungwhe. Paratype in U. S. Natl. Mus.)
1931. *Drawida hehoensis*, Gates, *Idem*, 33:340.
1933. *Drawida hehoensis*, Gates, *Idem*, 35:443.

The type locality of this species was said to be "Villagio di Chiala 1400-1500 m (Carin Padaung o Asciuii Gheeu)." The district mentioned was not a political division and reference presumably was to some area inhabited by Padaungs seventy-odd years ago when Fea was collecting in Burma. It may have been almost anywhere between Leiktho Circle and Karenni. The village probably passed out of existence long ago. No information about it was obtainable in Burma and a better guess than that above could not be made by Italian missionaries stationed at the area in question.

All drawidas found on the Shan Plateau during 1925-1940 were referred to three species, *hehoensis, longatria* and *nepalensis*. The latter two are clearly distinguished from *beddardi*

by length of their male deferent ducts and by the genital markings as well as associated glands. The color mentioned by Rosa provides no clue and may have been unnatural (preservation was alcoholic). The dorsal pores supposedly present doubtless were the "small dark spots" noted by Stephenson in his material. The "labbra rigonfie" of the type may well have been tumescences such as occasionally were recognizable in *hehoensis*, around the secondary male apertures. With these clarifications there remains no morphological or distributional contra-indication to suppression of *hehoensis* as a synonym of *beddardi*.

D. barwelli, with which *beddardi* was mistakenly synonymized, was never found in Burma.

Each male pore of the classical authors opens into an invagination comparable to copulatory chambers of various pheretimas. The much smaller primary pore is at the free end of a penis pendent from chamber roof. The penis is protrusible through the secondary aperture and the chamber itself is eversible. Male porophores at maximal protrusion, presumably as during copulation, have the penes projecting from a thicker basal portion. External apertures of the spermathecae, no longer minute, are large enough to admit a distal portion (at least) of the porophore into what appears to be a thickening of a parietal portion of the spermathecal duct. This chamber has been called an atrium but the structure bearing that name in many species of *Drawida*, although much larger, does not serve as a vagina.

Drawida bullata Gates 1933

1933. *Drawida fucosa* Gates, Rec. Indian Mus., 35:439. (Type locality, Kalewa, Burma. No types.)

Prome, September, 2-26-4. K. John.

Laboo (Prome), September, 0-0-13. K. John.

Thanbula (Thayetmyo), September, 12-30-46. K. John.

Taungdwingyi (Magwe), August, 0-0-12. K. John.

Minbu, August, 13-27-10. K. John.

Ye-U (Shwebo), August, 13-27-10. Saw San Thwe.

External characteristics. Size (juveniles excluded), 65-95 by 4-5 mm. (Minbu), to 94 by 4 mm. (Taungdwingyi), 55-65 by 3-4 mm. (Ye-U), 84-120 by 4-5 mm. (Laboo), 90-180 by 4-7 mm. (Thanbula), 150-180 by 4-7 mm. (Prome). Unpigmented. Nephropores, present from iii, on anterior margins of segments, at or close to *D.* Clitellar coloration, red, extending into ix and xiv.

Spermathecal pores, very small transverse slits, just median to *C*. A marginal area, forming a circumferential lip, is clearly marked off peripherally and often is so protuberant that the pore appears to be located on a transversely elliptical, small papilla. This usually seems to be segmental as it is bounded posteriorly by 7/8 but may be situated exactly on 7/8 with no more indication of belonging to vii than to viii. Only an anterior portion of such a lip is marked off, on most Minbu worms, by a transverse groove, concave posteriorly, that does not pass into 7/8. These lips or protuberances may be only slight eversions of the spermathecal ducts rather than definite porophores. Female pores, minute, circular, in transverse areas of greyish translucence, at or just lateral to *B*.

Male pores, transverse slits on ventral ends of whitened, anteroposteriorly flattened, rather pointed protuberances in *BC*, with median margins nearer to *B* than lateral margins are to *C* and often reaching *B*. Each porophore is bounded posteriorly by the presetal secondary furrow of xi and in front apparently (most specimens) by 10/11 which curves anteriorly around the porophore. On other worms 10/11 seemingly is continued just onto the median and lateral faces of the porophore where it becomes unrecognizable, the porophore bounded anteriorly by a groove that opens into 10/11 just beyond those blind endings. On such worms the male pore is in line with 10/11 and the porophore accordingly appears to be formed from parts of both x and xi though that from x is much the smaller. Porophores on other worms appear to belong wholly to xi, the male pores much nearer anterior than posterior margins. The porophore is delimited anteriorly, in Taungdwingyi worms, by a transverse furrow near posterior margin of x that does not pass into 10/11 but here also the larger part of the porophore obviously is from xi. Solid or other definite glands always are lacking in porophores of this species.

Genital markings, whitened areas of epidermal thickening, distinctly delimited as a rule but not associated with special glands, in (viii)-ix-xii (cf. Table 1). Markings of x usually are paired: transversely oval and with pointed end mesially, in median half of *BC* but sometimes reach *A* or into *AA*, in the postsetal annulus (Minbu, Taungdwingyi); longitudinal, reaching to or almost to *B* and *C* and through setal-postsetal annuli (Prome, Laboo, Thanbula, Ye-U) or confined to postsetal annulus (1, Ye-U). Paired markings of xi are transverse,

usually smaller than in x, in a median part of *BC* but occasionally reaching *A*, confined to setal or to setal-postsetal annuli. Unpaired and median markings are transverse, usually extending through setal-postsetal annuli (in which case the presetal annulus is quite short), reaching well into *BC* or even to *C*. A pair of markings that do not quite meet at mV, in viii of one Laboo worm and in ix of one Minbu worm, if united would be of the same size as the unpaired markings. On the right side of a Thanbula worm the marking of x is small and transverse but the marking of xi is large and longitudinal, the reverse of the usual condition as well as of that on the left side.

Internal anatomy. Gizzards, 1-3, in xv-xviii (Table 2). Three gizzards of a Prome specimen that may prove to belong to this species are in xviii-xx.

Testis sacs, usually unconstricted, about equally in ix and x. Vas deferens, slender, usually iridescent in 9/10 and in ix, in a number of short loops on anterior face of 9/10 median or close to or around hearts of ix. Occasionally, further loops (Minbu) are bound by connective tissue in a small cluster against posterior face of 9/10. A more ectal, non-iridescent and seemingly thickened portion in x, less than 5 mm. long, is slightly sinuous, zigzagged or in several short loops and passes into ental end of prostate directly. The cluster of hairpin loops of the thickened portion in x of worms from other localities may be about half the size of the testis sac above it (Ye-U, Prome), smaller to nearly as large (Thanbula), as large to larger (Laboo, Taungdwingyi). The thickened portion in a Ye-U worm is 60+ mm. long. Prostates, protuberant into coelomic cavity and usually bent over towards the nerve cord, narrowed only within the parietes, ental end bluntly rounded, shortly elliptical in cross section, occasionally with an appearance of slight anteroposterior flattening, glandular investment continued to body wall. Capsule, usually reddish, soft, digitiform, slightly curved, 1 (Taungdwingyi, Minbu) to 2 mm. (Prome, Thanbula) long.

Spermathecal atria, digitiform, in vii. Atria are erect on anterior face of 7/8, irregularly constricted or very shortly zigzag-looped and less than 5 mm. long (Minbu), or are in a clump of shortly u-shaped loops bound to ventral parietes. The cluster may be small and ventral or large enough to reach to or almost to dorsal parietes. Length, 10-20 mm. (Ye-U), 10-12 (Prome), 15-20 (Taungdwingyi), 60-70 mm. (Laboo). A terminal portion about 10 mm. long in some Laboo worms is filled with

a sticky white material in which slight spermatozoal iridescence is visible.

Ovarian chamber, closed off from parietes. Ovisacs, extend into xiv or xv.

Juveniles. Greyish translucent spots, anlage of male pores, are at 10/11 in the two smallest juveniles on which no porophores or protuberances are recognizable. Male porophores of larger juveniles are represented by slight swellings of anterior margin of xi without definite posterior demarcation, the pores now apparently behind 10/11 which seems to be bent forward slightly around the protuberances. If segment x contributes any part to the male porophore it certainly must be much smaller than that from xi.

Juveniles still without genital markings have male gonoducts of about the same length as those of aclitellate and clitellate worms from the same locality.

Remarks. The smallest adults are from a southern portion of the species range where there is considerable rainfall. The largest were found in regions of much less precipitation.

Some aclitellate worms (3 Taungdwingyi, 2 Ye-U, several Thanbula) appear otherwise to be fully mature.

From the postseptal portion of male gonoducts, in worms softened after long formalin preservation, a sheath had separated off so as to reveal internally a slightly zigzagged or sinuous tube of about the same thickness as the preseptal portion.

Male porophores have been seen only in a protuberant state, presumably just as at copulation. Information as to the completely retracted state is needed.

D. fucosa was distinguished from *bullata* by quantitative differences such as soma size, length of spermathecal atria and of male gonoducts. Individuals as small (20-45 by 1½-2 mm.) as most of those on which *bullata* was erected are unlikely to copulate with worms as large as the types of *fucosa* (130-170 by 6-7 mm.) but intermediate soma sizes herein reported make retention of *fucosa* unnecessary. Variation in lengths of spermathecal atria and vasa deferentia parallels that recorded below for *longatria* from which *bullata* is distinguished by absence of solid GM glands. Relationships to *vulgaris* remain uncertain.

Abnormality. (No. 1.) Left spermatheca, with two ampullae (distended by white material), one attached to posterior face of 7/8 in usual manner, other hanging down in coelomic cavity, each with a discrete duct 1½ mm. long, the united duct passing ventrally as usual.

TABLE 1

Frequency distribution of segmental position of median and paired genital markings in *D. bullata*

	Median Segments				Paired	
	ix	x	xi	xii	x	xi
Prome (30)					30	30
Laboo (13)	7		3	1	13	10
Thanbula (76)	11		4	19	76	72
Taungdwingyi (12)	12				12	12
Minbu (37)	25			8	37	37
Ye-U (9)	3	2		3	7	9

Figures in parentheses, number of specimens from the locality.

TABLE 2

Frequency distribution of segmental position and number of gizzards in *D. bullata*

TABLE 2

Locality	Segments				Number of gizzards		
	xv	xvi	xvii	xviii	1	2	3
Taungdwingyi	5	12			7	5	
Ye-U	9	11	2			11	
Minbu	14	27	28	2		13	5
Laboo	2	11	12	3		8	4
Thanbula	2	15	18	7		15	4
Prome	5	17	18	12		5	14

DRAWIDA CAERULEA Gates 1926

Kayan (Hanthawaddy), August, 0-5-8. K. John.
Thongwa (Hanthawaddy), August, 0-6-8. K. John.
Thinbawgyin (Bassein), October, 0-0-6. K. John.
Pegu, August, 0-0-2. "Jungles to the east," 0-3-1. K. John.
Thanatpin (Pegu), August, 0-2-3. K. John.
Toungoo, October, 0-2-0. K. John.
Minbu, August, 0-0-2. K. John.
Myingyan, September, 0-0-2. K. John.
Myotha (Sagaing), September, 0-1-1. K. John.
Ava (Sagaing), September, 0-3-6. K. John.
Mandalay, September, 0-7-0. K. John.
Ye-U (Shwebo), September, 0-9-34. Saw San Thwe.

External characteristics. Nephropores, present from iii. Left male porophore of one Kayan worm is completely retracted though the right is completely everted. Genital markings, always lacking.

Internal anatomy. Pigment, always present in the body wall. Gizzards, one or two only in Ye-U specimens, with one exception and then three in xiv-xvi. Commissures from extra-esophageals, behind 8/9 (60 specimens).

Vas deferens, slender, iridescent, twisted into a small cluster of loops that are firmly bound together (southern localities), slightly thicker throughout but still iridescent and loops much less firmly bound together (Ava), slightly thickened and iridescent throughout but longer and loops easily separated, length 65-70 mm. (Ye-U).

The spermathecal duct of southern worms obviously is more thickened in a terminal portion than in species of the *beddardi* group. The thickened part is pyriform or almost conical and mainly in the body wall. In Ye-U worms the thickened portion is asymmetrical and reaches forward halfway to 6/7 and presumably must be called an atrium. Size of the atrium is less than half that of *rasilis* in which 6/7 and dorsal parietes are reached.

Ovisacs may extend as far back as into region of xix-xxii.

Abnormality. (No. 2.) Left male porophore, at 9/10. Left male organs, one segment anterior to usual location. Ovarian chamber, in two discrete halves, on the left side one segment anterior to usual location as is the female pore. An ovisac extends posteriorly from each ovarian chamber. Left spermatheca, lacking.

The left mesoblastic somite at the eighth level presumably was aborted during early embryonic development and its place was taken by the one at the ninth level.

Regeneration. Tail regenerate, of eight segments at 136/137.

Remarks. Data as to number and location of gizzards in specimens listed above were lost, as well as records that would have permitted characterization of prostates more adequately than in the past.

Male porophores of all previous southern specimens were fully protruded. Maximal protrusion and complete retraction now has been shown by a single worm (Kayan). The thick-walled muscular chamber into which the terminal half of the protruded porophore is withdrawn has been considered to be a prostate. This chamber is distinguished from the prostates of most moniligastrids by absence of a glandular layer on its coelomic face. Pending acquisition of further information about both kinds, the term prostate with characterization of "muscular" is retained.

Whether a porophore as large as that of southern worms can be inserted, without change of form, into the spermathecal atrium seems doubtful. The ejaculatory apparatus certainly appears to be highly evolved even though a discrete penis (such as is present in *beddardi*) is lacking. The atrium in *rasilis* is much larger than is required for reception of the porophore of southern worms but the protruded condition has not been seen in northern worms. Atria of *decourcyi* Stephenson, 1914, are even larger but here again only the retracted state of the male porophores has been seen.

Atrium now seems a more appropriate characterization for the parietal invagination into which the spermatheca opens through an aperture on a discoidal genital marking. The primary spermathecal pore may prove to be within the atrium and if so the external aperture will be tertiary rather than secondary.

Southern worms were distinguished from *rasilis* mainly by quantitative differences such as length of vasa deferentia and size of spermathecal atria. The range of *D. caerulea caerulea* as now known is from the Irrawaddy delta to latitude of Mandalay. *D. caerulea rasilis* was found in the Chindwin valley near Monywa. Worms from the region of Mandalay to Ye-U and Monywa are intermediate with respect to one or another of the characters distinguishing the two subspecies. Considerable searching through difficult territory much farther north may be required to reveal whether intermediate forms exist between *caerulea* and *decourcyi*.

Drawida delicata nom. nov.

1930. *Drawida* sp., Gates, Rec. Indian Mus., 32, 298.

Remarks. A filament at distal end of each male porophore may be only euticular lining of the spermiducal passageway that had been loosened and then evaginated during strong contraction at preservation. Whether such contractions protruded discoidal porophores normally extending into x-xi or everted small parietal invaginations is unknown. A "blueish shade" may not have been associated with pigment any more than in the unpigmented lumbricid, *Octolasium cyaneum* (Savigny, 1826). The "minute" size of spermathecal ampullae and shortness of ovisacs (in xii) may or may not be indicative of immaturity.

The species is distinguished from *beddardi* by the greater length of male deferent ducts, by absence of parietal invaginations at ectal ends of male deferent apparatus or, if male porophores are everted chambers, by absence therein of protrusible tubular penes. Elongation of the male gonoducts also distinguishes *delicata* from all other Burmese species with adiverticulate spermathecae except *spissata*. The latter requires no consideration because of great differences in spermathecae and prostates. Relationships presumably are with species yet to be collected in the little known areas west and south of Mergui district.

Drawida flexa Gates 1929

Zinba (Tavoy), September, 0-0-1. W. D. Sutton.
Siyigyan (Tavoy), "plains" September, 0-1-3. W. D. Sutton.
Kawletchaung (Tavoy), "nearby hills," September, 0-4-5. W. D. Sutton.
Pyinthadaw (Tavoy), "nearby hills," September, 0-2-1. W. D. Sutton.
Nyaungdon (Tavoy), September, 0-0-1. W. D. Sutton.
Migyaunglaung (Tavoy), "plains," September, 0-1-0. W. D. Sutton.
Thaton, September, 0-0-2. K. John.
Duyinzeik (Thaton), September, 0-14-7. K. John.
Naunggala (Thaton), September, 0-3-3. K. John.
Bilin (Thaton), September, 0-15-12. K. John.
Taungzung (Thaton), September, 0-8-15. K. John.
Kinmunsakhan (Thaton), September, 0-0-7. K. John.
Boyagyi (Thaton), September, 0-1-0. K. John.
Kyaikto (Thaton), September, 0-12-4. "Nearby hills," September, 0-8-15. K. John.
Sittang (Thaton), October, 0-2-0. K. John.

External characteristics. Size may be rather small, as in worms from Kyaikto hills, 50-80 by 3-4 mm. (diameter measured across clitellum which is much wider than the rest of the worm). Nephropores, present from iii, in anterior margins of segments, usually at or close to *D*, pores of viii always dorsal to *D*, pores of ix usually at or only slightly dorsal to *D* but occasionally one or both dorsal and, more rarely, even farther from *D* than in viii. Dark spots at mD and near some preclitellar intersegmental furrows may look more or less like dorsal pores but epidermis and cuticle are imperforate even when there seems to be a gap in the musculature. Clitellar coloration, lacking ventrally on x and a presetal portion or all of xi, from a level just beyond lateral margin of male pore lips. Laterally from that level the epidermis is quite tumescent.

Spermathecal and male pores, larger than nephropores, certainly larger than female pores and accordingly not minute, margins of pores almost never smooth. Spermathecal pores, just median to *C*, at 7/8 or (apparently) just in front of 7/8. Male pores, at 10/11, close to m*BC*, longitudinally or transversely slit-like or irregular, each at center of an indistinctly delimited but nearly circular, white and slightly tumescent area reaching to or nearly to *B*, to a tertiary furrow on postsetal secondary annulus of x and the presetal secondary furrow of xi. The porophore is usually divided into two portions by 10/11 but when tumescent the furrow may be indistinct or even unrecognizable, especially close to the pores. The portion in front of 10/11 is lacking in Sittang worms.

Genital markings, usually transverse, 2 to 20, located as follows: Median (unpaired and rarely longitudinal), presetal in viii and x-xii, postsetal in vii-x, occasionally in setal annuli of vii and x. Paired, in *BC*, presetal in viii-xii, postsetal in vii and x, in setal annuli of viii-xi, in median half of *BC* (postsetal markings of vii, presetal of x-xi, those in setal annulus of x), or with centers nearer m*BC*. Duyinzeik and Taungzun worms have 16-20 markings each.

Internal anatomy. Gizzards, three (4 specimens), four (55), five (10), in xvi-xxiii (Table 4). Commissures from extra-esophageals, in front of 8/9.

Vas deferens, short, slender, and for most part iridescent (clitellate specimens), in several loose loops on anterior face of 9/10, twisted around heart of ix, several further loops on posterior face of 9/10, an ectalmost portion 1-2 mm. long apparently slightly thickened and certainly without recognizable iridescence. Prostates, erect, recumbent or held against parietes by delicate strands, J- or U-shaped, entalmost portion of capsule only slightly or not at all widened.

Spermathecal atria, small, usually 1-2 mm. long, in Taungzun worms occasionally reaching a length of 3 mm. An ental portion, about half the length or slightly less, usually distended and with thin wall. Lumen gradually narrowed and wall thickened in ectalmost portion. Spermathecal duct, passing into posterior face of atrium in vii close to parietes.

Reproduction. Ampullary coagulum of clitellate worms usually is characterized by a rather brilliant iridescence presumably spermatozoal. Spots of iridescence also are clearly visible in the coagulum within distended ental portions of the spermathecal atria in several Taungzun worms. Iridescence of male gonoducts

Table 3

Location of genital markings in *Drawida flexa*

Locality	Paired											Unpaired								
	Presetal					Setal				Postsetal		Presetal				Setal	Postsetal			
	viii	ix	x	xi	xii	viii	ix	x	xi	vii	x	viii	x	xi	xii	x	vii	viii	ix	x
Taungzun	15	18	13	8	10	17	10	23	11	11	1	15	6	13	1	9	11	1	18	8
Bilin	—	3	16	16	11	16	8	22	6	13	—	—	4	3	13	—	—	—	13	—
Duyinzeik	—	4	8	5	7	10	—	8	—	2	—	1	7	11	—	—	1	—	1	—
Kinmunsakhan	—	1	7	2	5	4	—	3	2	2	—	—	—	—	—	—	—	—	—	—
Kyaikto	—	4	3	6	6	5	—	6	2	1	1	5	7	5	—	—	2	—	—	—
Naunggala	—	—	1	2	2	1	—	3	2	—	1	—	—	2	2	2	1	—	—	—
Hills 1½ miles from Kyaikto	—	4	—	17	13	6	3	7	—	1	1	—	12	14	4	—	8	13	—	—
Sittang	—	1	1	1	—	—	1	1	—	—	—	1	2	—	1	—	—	1	—	—
Kyaikto	—	5	2	—	—	2	—	1	1	—	5	—	1	2	—	6	—	2	1	1
Kyaikto town	—	5	6	12	3	6	—	10	3	—	2	1	2	6	8	1	—	—	1	—
Thaton	—	—	2	2	2	—	—	—	—	1	—	1	—	—	—	—	1	—	—	—
Tavoy No. 1	1	3	2	—	1	3	1	3	—	—	3	—	4	2	—	—	—	—	2	1
" No. 2	5	5	3	3	1	1	1	—	—	—	6	—	7	7	—	1	—	—	3	—
" No. 3	2	2	2	1	2	2	—	3	—	—	3	—	3	3	—	1	—	—	—	—
" No. 4	2	4	2	1	1	2	1	—	—	—	3	—	5	3	—	1	—	—	—	—

Localities of numbered batches from Tavoy district cannot now be stated. The key, as well as the specimens, were destroyed during the war in Burma.

presumably is due to presence of sperm on the way out from the testis sacs. As sperm are matured and exchanged in copulation, reproduction is assumed to be sexual and biparental.

Regeneration. The only record now available is of a tail regenerate, at 170/171, with terminal anus and 36+ segments.

The difference in thickness of ectal and ental portions of spermathecal atria, and of the shape, is so little that the organ can be called digitiform. A similar slight distention of an ental portion sometimes was recognizable in much longer atria of *bullata* and *longatria.*

The *flexa* range in Burma appears to be restricted to the Tenasserim division and there from Tavoy north to the Sittang River. The Thailand boundary may not be a natural boundary for the species.

Relationships are with *longatria* from which *flexa* is distinguished by the smaller genital markings, smaller size of the glands associated with those markings, absence of a gland in male porophores and shortness of spermathecal atria. Atria are of about the same length in several races of *longatria* but not in those found in the *flexa* range. Additonal differences may be recognizable when retracted states of *longatria* male porophores can be seen. Although differences are quantitative, all specimens from the Tenasserim division have been referable, without question, to one or the other of the species involved.

TABLE 4

Frequency distribution of segmental position and number of gizzards in *D. flexa*

Locality	Segments								Number of gizzards		
	xvi	xvii	xviii	xix	xx	xxi	xxii	xxiii	3	4	5
Duyinzeik (17)	1	6	12	17	17	15	3		2	10	5
Taungzun (22)		6	17	21	22	18	6		1	18	3
Pyinthadaw (3)		2	3	3	3	1				3	
Naunggala (6)		1	5	5	6	6	2		1	3	2
Kawletchaung (9)		4	8	8	9	5	1	1		9	
Siyigyan (4)		1	4	4	4	3				4	
Miscellaneous* (8)		2	7	8	8	6	1			8	
Totals	1	22	56	66	69	54	13	1	4	55	10

* Includes: xvii-xx (1 Migyaunglaung, 1 Thaton),
xviii-xxi (2 Sittang, 1 Thaton, 1 Boyagyi, 1 Zinba),
xix-xxii (1 Nyaungdon).

Drawida gracilis Gates 1925

Thaton, September, 23-0-0. K. John.
Kyaikto (Thaton), September, 1-0-0. K. John.
Thongwa (Hanthawaddy), August, 24-4-0. K. John.
Twante (Hanthawaddy), September, 1-0-0. K. John.
Hlawga (Insein), September, 4-0-0. K. John.
Wanetchaung (Insein), September, 5-0 0. K. John.
Taukkyan (Insein), September, 7-1-0. K. John.
Thinbawgyin (Bassein), October, 0-3-0. K. John.
Pegu, August, 38-0-0. "Jungle to the east," 60-0-0. "Jungle to the west," 33-0-0. K. John.
Thanatpin (Pegu), August, 9-0-0. K. John.
Paukkaung (Prome), September, 9-0-0. K. John.
Prome, September, 11-0-1. K. John.
Thanbula (Thayetmyo), September, 5-3-0. K. John.
Sandoway, "Hills," September, 19-0-0. I. M. Ismailjee.
Ramree (Kyaukpyu), "nearby hills," September, 1-0-0. I. M. Ismailjee.

External characteristics. Nephropores, present from iii. Clitellar coloration, red, lacking ventrally on x and presetal half of xi. Male porophores of the clitellate specimen are protuberant, rather conical but with rounded distal ends. firm but containing no glands. Porophores of less mature worms are more nearly discoidal but possibly because adult organization had not been completely achieved.

Genital markings, indistinctly delimited areas of epidermal thickening, paired, transverse, between *B* and a level just beyond lateral margin of male porophores, in the presetal annulus of x, anterior portion of the postsetal annulus of x, setal annulus of xi but extending forward into presetal annulus and occasionally almost to the intersegmental furrow. Markings in x of the clitellate specimen meet mesially, a slight furrow along mV the only indication of a boundary. The ventral setae are included in the anterior markings. The epidermis in a presetal portion of ix (Prome, clitellate) or viii and ix (Thongwa, aclitellates) is thickened in *BB* or even *CC* but no markings are recognizable externally. A longitudinal marking, in a median portion of *BC* (3 Pegu specimens), extends through the whole length of x as on one of the types.

Internal anatomy. Gizzards, two (1 specimen), three (26), four (6), in xiv-xx (Table 6). Intestinal origin, in xxi (specimen with gizzards in xiv-xvii), just behind 21/22 (specimens with gizzards in xiv-xvii and xiv-xvi). Commissures from extra-esophageals, in front of 8/9.

Vas deferens, slender, rather long, twisted into two clusters of closely compacted loops, one on each face of 9/10, clusters of about the same size or the anterior slightly larger, the two together smaller than the testis sac, slender throughout. Prostates, sessile on parietes, of circular outline, capsule small, 0.5-1.25 mm. long, shortly ovoidal, pointed end within the parietes.

Spermathecal atria, digitiform, 1.0-1.5 mm. long, lumen narrow, an irregular cleft in transverse section. Ovisacs (clitellate worm) reaching into xvii.

Abnormality. (No. 2.) Male porophores, two pairs, on 10/11 and 11/12, each porophore with a minute, transversely placed male pore. Greyish translucent spots in 11/12 at *B* just median to margins of male porophores are about at sites of female pores. Testis sacs of 9/10 are normal but in the region where 10/11 should be there is on each side of the body a fairly large cluster of loops of a second vas deferens that is not connected at all with the anterior male gonoduct. The prostate, on each side, is a single acinous mass extending slightly across levels of intersegmental furrows 10/11 and 11/12. The anterior vas of a side passes into the anterior margin, the second into the posterior margin of the prostate. Paired ovisacs extend into xiv.

Ovaries and oviducal funnels were not distinguishable, in part perhaps because of poor preservation. Relationships of septum 10/11 to 11/12, to the gut, and to the parietes were not determined.

Gonads of xi may have been hermaphroditic.

Remarks. Length of fully mature worms is unknown, since only anterior portions of aclitellate and clitellate individuals were obtained. Absence of mature specimens in collections from

TABLE 5

Frequency distribution of segmental position of genital markings in *D. gracilis*

Locality	Segments x presetal	x postsetal	xi
Thongwa	3	8	8
Taukkyan		6	6
Prome	7	7	7
Thanbula	2	2	2
Hlawga	2	2	2
Pegu	1	4	4
Paukkaung	3	3	3
Thinbawgyin		3	3

so many localities may have been due to failure to dig deep enough.

Some geographical variation in a range as large as that of *gracilis* would not be unexpected.

TABLE 6

Frequency distribution of segmental position and number of gizzards in *D. gracilis*

Locality	Segments							Number of gizzards		
	xiv	xv	xvi	xvii	xviii	xix	xx	2	3	4
Thanbula (3)	3	3	3						3	
Thongwa (7)	3	7	7	4				1	5	1
Pegu (15)	2	6	11	14	10	5	2		10	5
Prome (5)		4	5	5	1				5	
Taukkyan (1)			1	1	1				1	
Thinbawgyin (2)			1	2	2	1			2	
Totals	8	20	28	26	14	6	2	1	26	6

DRAWIDA LONGATRIA Gates 1925

External characteristics. Nephropores, obvious, present from iii, except on x of adults, at or very close to *CD* except in viii where they are somewhat more dorsal. A longitudinal dark band of rather blueish appearance (as if pigment were showing through the epidermis) usually is visible at mD except in the most anterior segments. Also visible at mD, close to various anterior intersegmental furrows, are markings that look more or less like dorsal pores.

Internal anatomy. A discrete longitudinal musele band at mD is lacking. Instead, the longitudinal musele layer gradually becomes thinner toward mD and just at that level is almost *non*-existent. This thinning is responsible for the externally recognizable dark band at mD. Close to intersegmental levels at mD, especially anteriorly, after stripping off the longitudinal museulature, there are visible slight protuberances or depressions but cutiele and epidermis are not perforated, i.e., dorsal pores are lacking.

The gut behind the pharynx is rather slender, in viii-x with low but lamelliform longitudinal ridges on inner wall. The gut is valvular, in individuals of the nominate race having gizzards in xv-xviii, through all of xxii or of xxiii.

The dorsal trunk is single anteriorly until disappearance into tissues of the pharyngeal bulb. The subneural, usually large

and blood-filled, is adherent to the parietes. Even before removal of the cord, the trunk usually is recognizable in contracted specimens as closed ends of the loops protrude beyond each side of the cord. Nephridia, apparently vesiculate behind the clitellum, bladders perhaps elongately sausage-shaped (condition poor and relationships of parts not determinable with certainty). Nephridial ducts, behind the clitellum at least, pass into parietes at *CD* gap. Nephridia were not found in x of adults and presumably are aborted prior to maturity. Brain and commissures to subpharyngeal ganglion were left posteriorly in iii by a transverse section exactly along 3/4.

Glands associated with genital markings have no lumen but are provided with a thick, tough and obviously muscular wall.

Remarks. As male porophores always have been more or less markedly protuberant the retracted states cannot yet be characterized. Because of appearances in specimens with less protuberance it is suspected that the primary male pores may be invaginated slightly in a state of complete retraction.

Supposed pores of GM glands, previously recorded, are now believed to have been artifacts. These "glands," without any lumen and thus called solid, may have mechanical rather than secretory functions, such as stiffening penes (certain Chinese species) or male porophores (*longatria*), gripping penes or porophores during copulation when present in walls of spermathecal pore invaginations (some Chinese species) or in the parietes close to the spermathecal pores (*longatria*).

Internal anatomy of all specimens available since 1941 is like that of the nominate race as characterized above.

Variation in shape, size and direction of male porophores, in size, shape and location of genital markings, is so great that attempts to define a few externally identifiable varieties were abandoned long ago. Many large collections from the recent alluvium in the deltas region south of Henzada-Tharrawaddy, secured after 1932, contained only individuals that were like the Rangoon types on which the species was erected. This material enabled recognition of a location pattern for genital markings though many individuals lack one or more of the set. An area somewhat larger than that just indicated had been delimited, before Pearl Harbor, as the probable range of a nominate race. Presence of the same form in places as far apart as Rangoon, Burma and Palembang, Sumatra, must be attributed to overseas transportation, presumably by man. The original source

obviously is Burma. Since habits are such as to permit transportation, and colonizing ability had been demonstrated, it was then possible to assume that presence of the nominate race in isolated Burmese localities such as Myitkyina, Bhamo, etc., likewise is a result of transportation. Disregarding such colonies which appeared to be localized in and immediately around towns to which potted plants are known to have been taken from Rangoon, delimitation of ranges of other races, usually found in less urban situations, was under way when the Japanese invasion ended local study of Burmese earthworms.

The races differ from one another in various characters, some of which are determinable only from dissection. Some of the differences have been thought to distinguish species. Male porophores probably are not exactly the same in any two races of which there are an unusual number.

Drawida longatria longatria Gates 1931

External characteristics. Segments, 183 and 206, the last few metameres of each worm very small, without externally recognizable setae but showing no evidence of regeneration.

Spermathecal pores, not minute, transversely slit-like.

Genital markings: unpaired, median, presetal, in *AA*, of xi (6 specimens), xii (16), xiii (7); paired, each in median half of *BC* in xii (3), united marginally with a median marking (2), or rudimentary (1). An area of greyish translucence, in lateral half of *BD* or even reaching beyond *D*, in presetal annulus of viii lacks the distinctly demarcated rim of the other markings but is associated with a characteristic parietal gland. A less obvious area of epidermal modification, associated with a small gland, is present in the posterior part of vii just median to each spermathecal pore.

Regeneration. Three of the sixteen worms from Bhamo and Myitkyina, with 124, 171 and 172 segments, are unregenerate posterior amputees. Another individual had lost its hind end at time of collection. Ten of the twelve remaining specimens have tail regenerates. Number of segments in the regenerates: at 104/105, 86 setigerous + several very short and without externally recognizable setae; at 124/125, 23 + 7 or more; at 136/137, 14 + 6 or more; at 143/144, 16 + 6 or more; at 165/166, 6 + ?. The anus in each of those cases is terminal. Young regenerates at 142/143, 145/146, 151/152 and 152/153 each have a dorsoterminal anus that may reach nearly to the substrate.

Segments, usually without externally recognizable setae, usually are distinguishable only on the ventral side. The distance from substrate to dorsal margin of the anus, in a regenerate with indications of 10 + segments, is only about a quarter of the distance from substrate to ventral margin. One regenerate, at 196/197, is unsegmented.

Remarks. The two unamputated worms, with 183 and 206 segments, obviously had become sexually mature before metameric differentiation had been completed in a terminal portion of the body.

External characteristics. Length of worms from Tharrawaddy district, to 170 mm. Diameter, to 7 mm. Segments, 149 + a number of rudimentary metameres without externally recognizable setae, 177 + 1 or 2, 190 + several (3 specimens), 191 + 2 or more, 193 + 1 or 2, 206 + 2 or 3, 210 + 2, 211 + 2 (2 specimens), 220 + several.

Genital markings: unpaired, median, presetal, in *AA* of xii (2 specimens); paired, each in median half of *BC* or reaching to *A*, presetal, in xii (32), in viii where margin is indistinct as in Bhamo-Myitkyina worms (41), occasionally replaced by two or even three smaller markings, postsetal, in lateral part of *BC* in vii (41) and there small, even more indistinct than in viii.

Regeneration. Three worms are unregenerate posterior amputees. Thirteen worms had lost their hind ends at or since time of collection. Six of the remaining twenty-five have tail regenerates as follows: still unsegmented, anus reaching forward in dorsum nearly to substrate; anus dorsoterminal, segmentation indicated ventrally but setae unrecognizable externally; at 134/135, 10 setigerous segments + a number on which setae are unrecognizable, anus dorsoterminal; at 143/144, 12 + several; at 191/192, 3 + several; at 197/198, 5 + several.

Remarks. Each of the 19 unamputated worms has, immediately in front of the anal segment, one or more circumferential furrows that presumably are intersegmental. In the axial portions thus delimited, nephropores and setae are unrecognizable. The portion of the body in front of the anus then is a growth region in which metameric differentiation had not been completed when the worm became sexually mature.

These Tharrawaddy worms probably were secured in the plains.

Drawida longatria verrucosa Gates 1931

External characteristics. Segments, 205, 206, 213, 224, 225, 233, 237, 238, in each case with two or more rudimentary segments already demarcated but without externally recognizable setae.

Spermathecal pores, like the male apertures, small transverse slits. Male pores, facing anteriorly or anterolaterally. Tumescent margin of the male pore with a slight but definite groove coming out of the pore and passing posteriorly on ventral face of the tumescence. Male porophores, in *AD*, reaching equators of x-xi or shortened at either end. Each disc-like porophore may have an anterior and a posterior genital marking, or markings may scarcely be distinguishable though glands are present, or either marking and the gland may be absent.

Genital markings, additional to those of the male porophores, are as follows. Unpaired, median, in *AA*, presetal in viii (3 specimens), in setal annulus of viii (3), postsetal in x (11), xi (13), xii (17). Paired, presetal in *AA* of x (2, in *AB* of viii (3), x (13), xi (2), postsetal in x (15); larger and in some part of *AD* on each side, postsetal in vii (17), postsetal in viii (15, in two of which each marking is replaced by two smaller ones), presetal in x (4), presetal in xii (14).

Regeneration. One worm is an unregenerate posterior amputee and another had lost part of its tail at time of collection. Four have tail regenerates. One has no externally recognizable segmentation. Another, also with a dorsoterminal anus has several rudimentary segments (without setae) marked off ventrally. Two regenerates, at 198/199, have each a terminal anus; segments, 6 (+?) and 19 (+?).

Remarks. Each of the eleven unamputated worms has several rudimentary segments at its posterior end.

This series of seventeen specimens from Tharrawaddy district probably was secured in the hills or in jungles remote from the town.

Drawida nana Gates 1933

The GM glands have a soft, opaque wall without muscular sheen and may represent an intermediate stage in evolution from the "clear" sort with transparent wall to the *longatria* sort with a strongly muscularized wall. If, however, definite pores are present in the associated genital markings, as was originally believed, the glands will not be solid and will provide additional evidence for distinction from *longatria*.

Drawida nepalensis Michaelsen

1907. *Drawida nepalensis* Michaelsen, Mitt. Naturhist. Mus. Hamburg, 24:146. (Type locality, Gowchar, near Katmandu, Nepal. Type in the Indian Mus.)
1909. *Drawida nepalensis* + *D. burchardi* Michaelsen, Mem. Indian Mus., 1:147, 149.
1916. *Drawida jalpaigurensis* Stephenson, Rec. Indian Mus., 12:307. (Type locality, Jalpaiguri, at base of the eastern Himalayas. Type in the Indian Museum.)
1917. *Drawida nepalensis*, Stephenson, Rec. Indian Mus., 13:372.
1922. *Drawida nepalensis*, Stephenson, *Idem*, 24:430.
1923. *Drawida nepalensis* + *D. burchardi* + *D. jalpaigurensis*, Stephenson, (The Fauna of British India), Oligochaeta, p. 146, 134, 141.
1924. *Drawida troglodytes* Stephenson, Rec. Indian Mus., 26:129. (Type locality, Siju Cave, Garo Hills, Assam. Type, in the Indian Mus.)
1925. *Drawida burchardi* + *D. hodgarti* + *D. papillifer* (part), Stephenson, *Idem*, 27:50, 51.
1926. *Drawida cacharensis* Stephenson, *Idem*, 28:251. (Type locality, Katlicherra, South Cachar, Assam. Types, in the Indian Mus.)
1929. *Drawida nepalensis*, Stephenson, *Idem*, 31:229.
1930. *Drawida nepalensis*, Gates, *Idem*, 32:290.
1931. *Drawida nepalensis*, Gates, *Idem*, 33:348.
1933. *Drawida burchardi*, Gates, *Idem*, 35:426.
1934. *Drawida nepalensis* + *D. troglodytes*, Gates, *Idem*, 36:242 and 253.

Andaman Islands

Port Blair, Station B 10, 2 specimens. Station B 15, 0-1-0. (Indian Mus.) Station 6, 1-0-0. (Indian Mus.)
(No station indicated), September 1932-May 1933, 0-1-0. H. S. Rao. No data, 0-1-0. (Indian Mus.)

Burma

Sandoway, riverside, September, 0-1-0. Hills, September, 0-6-1. I. M. Ismailjee.
Akyab, September, 0-16-17. I. M. Ismailjee.
Myohaung (Akyab), September, 0-0-7. I. M. Ismailjee.
Naba (Katha), nearby hills, September, 0-2-0. Saw San Thwe.
Lashio (Northern Shan States), 7th mile on the Namtu road, September, 0-3-15. Wan Hu Mone village, 5 miles from Lashio, muddy ground covered with water cress, September, 0-0-1. H. Young.
E Nai village (North Hsenwi State), 9 miles from Lashio, at base of bamboo clumps, September, 0-5-20. H. Young.
Bhamo, September, 0-4-8. K. John.
Myitkyina, September, 0-0-14. K. John.
Weshi (Myitkyina), October, 0-3-0. F. D. Forbes.

India

Lokra (Balipara Frontier Tract, Assam), 8.xi.1939, 0-2-0. S. L. Hora (Indian Mus.)

Teesta Bridge, Teesta Valley, 2/6/34, -49-1. S. L. Hora (Indian Mus.)

Nagrota (Kulu District, Punjab), garden of P. W. D. rest house, 13/6/26, 0-1-0. S. L. Hora (Indian Mus.)

Pakistan

Lahore and vicinity, 29-16-13. H. K. Bhatti.

External characteristics. Size (Pakistan), 78-105 by 4-5 mm. Segments (Pakistan), 86 (posterior amputee), 113 (p. a.), 114 (p. a.), 129, 130, 137, 138, 139, 140, 144, 153, all juvenile, 135, 145, 148, 150, 154, 156, 157, 158, 159, 161, 162, 163, 164 (2 specimens), 166 (2), 168, 169, 173, 176, aclitellate and clitellate specimens. Setae (Pakistan), closely paired, $AB = CD$, $AA > BC$, DD ca. $= \frac{1}{2}$C, unrecognizable in last three or four segments. Nephropores, present from iii, at *D* except slightly more dorsal on vii (Pakistan) or vii-viii (Burma), usually lacking (or unrecognizable?) in x (Burma) or x and xii (Pakistan) though quite obvious in xi. A pore definitely is present on right side of xii (1, Pakistan) and vestiges of pores of x sometimes become visible after treatment with picric acid.

Male porophores of most specimens are as previously described by the author and in a condition that must now be regarded as of maximal or near maximal protrusion, presumably as during copulation. Porophores of one Pakistan worm, almost if not fully retracted, are circular to shortly elliptical areas distinctly delimited from x and xi, depressed slightly below general epidermal level. Segments x and xi are slightly indented so that short anterior and posterior portions of the porophore are concealed from view. More indentation, if further change is possible, presumably would result in complete coverage of porophores which might then appear to be in some sort of a chamber.

Genital markings are of at least two sorts. 1) Small, circular areas of greyish translucence, one in each male porophore and one in vii just in front of each spermathecal pore. Around each of the anterior markings there often is a fairly wide and opaque band of slight epidermal thickening. The translucent area is the outer face of a nearly spheroidal solid "gland" filled with greyish translucent tissue. Porophore markings occasionally are not recognizable though the glands are present. Anterior glands may bulge the body wall up into the coelom or may be visible internally through gaps in the musculature. Glands of vii were

not found in several Arakan specimens but epidermis at sites of markings is slightly tumescent and wrinkled. 2) Areas of slight epidermal modification and not associated with solid or other glands. Two small transverse markings (Burmese worms) in each setal annulus of x and xi, about in line with the male porophores, epidermis slightly thinned. A median, transversely elliptical marking (many Pakistan worms) reaching *A* or *B* on each side in presetal half of xi, epidermis slightly thickened and without clitellar coloration. Paired, translucent areas of epidermal thickening in lateral part of *BC* or reaching *D*, presetal in vii (Lashio).

Five Arakan worms have a median presetal marking of variable shape and size in *AA* of ix. A central portion of each is translucent. Removal of the longitudinal musculature disclosed in the remaining thin portion of the body wall only a translucent spot which may be a vestige or rudiment of a gland.

Internal anatomy. A special longitudinal muscle band is lacking at mD where there is a gap in the musculature from 3/4 or 4/5 posteriorly that is of about the same appearance as those at setal levels. The gap is slightly widened just behind intersegmental levels. Removal of the longitudinal musculature discloses a slight protuberance at mD just behind level of each intersegmental furrow. The protuberance is over site of a somewhat pore-like marking which is behind rather than at intersegmental level. The cuticle and epidermis are imperforate, hence there are no dorsal pores.

A low rather broad median ridge is present on the floor of the esophagus in middle segments of the region behind the last gizzard. Gizzards, two to four (Table 7), in types of *cacharensis* are located as follows: xiv, xvi, xviii (2 specimens); xiv-xv, xviii (1); xiv, xvii-xviii (1); xiv, xviii-xix (1); xv, xviii (1); xvii, xix (1). Intestinal origin (Lokra worms), in xxiv (1 specimen), xxv (1), xxvi (3), xxvii (5). Enterosegmental organs in four or five postgizzard segments are especially obvious.

Dorsal blood vessel, probably complete but traceable only into iv. Ventral trunk, complete, bifurcating over subpharyngeal ganglion, the branches traceable along the circumpharyngeal nervous commissures nearly to the brain. Subneural trunk, adherent to parietes, traceable anteriorly only into x or ix. Commissures from extra-esophageals, in front of 8/9. From each posterior commissure a vessel may pass back on dorsolateral aspect of gut into xii or xiii, with four transverse connections

to the corresponding vessel of the opposite side. One of those paired vessels usually is unrecognizable, perhaps because it is empty rather than absent. The vessel that is visible is near the median plane and presumably is the one believed in the past to be a supra-esophageal. Hearts, of vi-ix lateral. Nephridia, lacking in x, vesiculate, bladder (usually called a caecum) elongately sausage-shaped. Nephridial ducts, pass into parietes at *D*.

One testis sac occasionally is displaced posteriorly underneath the ovarian chamber (13 Akyab specimens, neither sac displaced in 22 Akyab worms). Vas deferens, slender and iridescent in 9/10 and ix, with several small loops on anterior face of 9/10, one loop encircling heart of ix, thickened in x and there opaque, twisted into a cluster of loops that may be as large as the testis sac. Prostatic capsule, slenderly club-shaped, only very slightly and gradually widened entally, 2-4 mm. long.

Spermathecal atria, 3-5 mm. long, reaching into contact above gut or overlapping slightly, an ectal portion of variable length stalk-like, the widened ental portion usually irregularly constricted. Spermathecal ampullae (Pakistan), empty, translucent. Ovisacs (Pakistan), apparently reaching back into xiv-xv but actually within pockets of 12/13. Contents of distended ovisacs consist of yolk granules of several sizes. Ova, if at all present, certainly must be very few (aclitellate as well as clitellate worms). Female funnels, vertically elongated and band-like, on posterior wall of the chamber from parietes to opening into ovisac, lateral margins folded over toward each other so as to form a sort of trough almost closed. Ovaries (preservation poor) apparently band-like and placed vertically opposite the female funnels. No egg strings were found.

Juveniles. Male porophores, on most of the Teesta juveniles, are represented by very small swellings on which the pores but not the genital markings are visible. Each swelling is demarcated anteriorly as well as posteriorly by a slight transverse furrow that does not pass at either end into 10/11. The latter is continued, on each side of the porophore, nearly to the tip and the male pore. Deepening of intrasegmental grooves and extension to 10/11 along with obliteration of 10/11 in the porophore presumably would produce the appearance characteristic of adults, of belonging neither to x nor xi. The male pores now are assumed to belong morphologically at 10/11, with the porophores originating about equally from x and xi.

Testis sacs, in the smallest Pakistan juveniles, just below the gut, gonoduct loops about at site where the testis would be in

other families. Ovisacs in juveniles of some size still are unrecognizable and the ovarian chamber apparently is not closed off peripherally. Oviducal funnels are recognizable but ovaries were not found.

Abnormality. Five helicometameres are present in the intestinal region of a Pakistan worm.

Regeneration. Head regenerate of six segments at 6/7 (Myitkyina). Tail regenerate, 5 mm. long (Arakan).

Parasites. Crescent-shaped, uninucleate protozoans are present (Arakan worms) in numbers on the dorsal face of the gut near the dorsal blood vessel.

Remarks. Variation in segment number is similar to that of *longatria.*

Septa from 10/11 posteriorly though membranous are strong enough to allow considerable anteroposterior movement of a postgenital portion of the gut — in one Pakistan worm the gut of xii-xiv and including a gizzard is in front of the ovarian chamber. Preservation, in the case just cited, was such as to permit tracing septa to insertions on gut as well as parietes thus enabling recognition of morphological location of the gizzard. Septa in the postgenital region often are adherent to the gut beyond the real insertions which may not always have been identified correctly. Even if all discontinuities in the gizzard series are mistaken the condition responsible for the erroneous determinations is characteristic of many individuals of *nepalensis.*

Male porophores of adult worms previously identified as *nepalensis* by the author were markedly protuberant presumably as during copulation. One of the Pakistan worms now has shown the retracted condition of the porophores.

D. cacharensis is known only from the type series comprising 16 (3 previously dissected) aclitellate (?) specimens. Differences from *nepalensis* are restricted to the male porophores. When protuberant, the porophores are like those of the author's *nepalensis* or slightly more conical. The genital marking sometimes is unrecognizable but the solid gland is present. Retracted porophores are as in one of the Pakistan worms. Similar porophores of the unique type of *troglodytes* then are also in a retracted state. There now is no contra-indication to synonymization of *cacharensis* and *troglodytes. D. jalpaigurensis* has been known hitherto only from the original account of a single aclitellate specimen "in a bad state of preservation." Examination of the type some years ago provided the data recorded below.

Addendum

External characteristics. Spermathecal pores, transverse slits at 7/8, slightly median to *C*. Male pores, not recognizable. Male porophores, transverse, very slightly raised, reaching mesially near to *B* and laterally at least to m*BC*, 10/11 continued slightly into the median margins but not into the lateral margins. Anteriorly and posteriorly each porophore is bounded by a definite, crescentic furrow concave towards the porophore, neither furrow passing into 10/11 mesially or laterally. A distinctly demarcated circular area just behind level of 10/11 in each porophore is the outer face of a tough-walled ovoidal gland protuberant into coelomic cavity, narrower and buried in the parietes. Genital markings, paired, presetal in vii, postsetal in vii and there just in front of each spermathecal pore.

Internal anatomy. Vas deferens, short. Glandular investment of the prostate, much thicker than the slender capsule. Spermathecal duct, in vii passing into posterior face near parietes of a saccular erect atrium. The gland of the postsetal genital marking of vii (labelled atrium in Stephenson 1923, fig. 51, p. 141) protrudes slightly into the coelom.

Remarks. Except for apparent shortness of the male gonoducts no evidence was found to justify retention of *jalpaigurensis*.

Forma ABSCISA Gates 1931

Kutkai (Northern Shan States), Dak bungalow grounds, *ca.* 4500 feet, November, 1926, 0-0-1. H. S. Rao (Indian Mus.).

Namkham (Northern Shan States), streams and pools on the north bank of the Shweli River, *ca.* 2500 feet, December 1926, 0-0-8. H. S. Rao (Indian Mus.).

Lashio (Northern Shan States), 0-3-0. H. Young.

Myitkyina and vicinity, September, 0-4-2. K. John.

Kadranyang (73rd mile on road from Myitkyina to Putao), October, 0-3-0. F. D. Forbes.

Kawa pang (82nd mile on same road), October, 0-5-0. F. D. Forbes.

Nawnghkai (250th mile on same road), October, 0-15-0. F. D. Forbes.

Hting bai (92nd mile on same road), October, 0-7-0. F. D. Forbes.

External characteristics. Nephropores, present from iii. Spermathecal pores, transverse slits with smooth margins (aclitellate specimens) exactly on 7/8. Male pores, very small transverse slits but quite obvious and in concave depressions of ventral faces of protuberant porophores.

Genital markings here also are of two sorts: 1) Associated with a solid gland as in *nepalensis*. Very small, circular, greyish translucent areas in vii-viii close to 7/8 and near the spermathecal pores. One marking always is present in the vicinity of each spermathecal pore but there may be one or two more. 2) Circular, opaque and indistinctly delimited markings, unpaired even though not median, with a small translucent central spot and not associated with glands. These markings are lacking on ten of the worms.

Internal anatomy. Gizzards, three to five in xiii-xix (Table 9). Commissures from extra-esophageals, in front of 8/9.

Reproduction. Spermathecal ampulla of previous specimens, even though elitellate, were in a juvenile condition. No sperm were found in the spermathecal atria or spermathecal ducts and no externally adhesive spermatophores (as in all other species of *Drawida*) ever were seen. Parthenogenesis was suspected but in *Drawida* recognition of male sterility is not as easy as in some other genera. Testis sac coagulum was examined for evidence of sperm but the data no longer are available.

Spermathecal ampullae of six aclitellate worms from Hting bai, Kadranyang and Kawa pang, are large enough to be considered of adult size. Each adult ampulla, except in one worm, is filled with a sticky white material which may have (2 specimens) a slight iridescence that presumably is due to presence of sperm. However, spermathecal atria appear to be juvenile, ovarian chambers are empty, and ovisacs are juvenile.

Remarks. Male porophores of all worms referred to *abscisa* were protuberant, presumably as in copulation. Though easily distinguishable from those of *nepalensis* in the protruded condition, little difference in shape or appearance is expected in completely retracted states. Differences of *abscisa* from *nepalensis* are mostly quantitative such as smaller size, fewer segments (?), absence of a solid gland in the male porophores. The seeming discontinuity of the gizzard series that characterizes a majority of specimens of *nepalensis* has not been found in individuals with *abscisa* male porophores. Both forms have been transported by man and the original home of each is unknown. The Myitkyina records do seem to suggest that the northern part of the district is near if not within the original range. However, other earthworms collected by Mr. Forbes between Myitkyina and Putao are all of peregrine species and all were secured in vicinity of government rest houses to which exotic plants in pots or tins are known to have been taken. Worms with *abscisa* characters have not been found outside of Burma.

The locality list might well have been much longer except for an unfortunate rivalry. The collections from a northern part of the Myitkyina district were made by a missionary after the end of the rains when earthworm activity (cf. Gates. 1960b) is mostly restricted to still moist sites. Certain reptiles being collected for a museum, at the same time and in the same area, had to be fed on earthworms. The missionary was getting too large a share of the limited supply wherever he went. A complaint lodged with the government that the missionary was a communist spy resulted in an order that he return at once to Rangoon.

TABLE 7

Location of gizzards and of intestinal origin in *Drawida nepalensis*

	Segments								
	xiii	xiv	xv	xvi	xvii	xviii	xix	xx	Locality
	1	1			1				Pakistan
	1		1		1				Lokra
		1	1		1			xxvi	Akyab
		3	3		3				Pakistan
		1	1			1		xxvi	Akyab
		1	1				1	1	Pakistan
		2		2		2			Pakistan
		1		1			1		Pakistan
			1	1	1			xxvi	Akyab
			1	1	1			xxvii	Akyab
			1	1	1			xxviii	Akyab
			1	1	1				Lokra
			1	1		1		xxvi	Akyab
			1	1		1		xxvii	Akyab
			1	1			1	1 xxvi	Akyab
			1		1				Pakistan
			1			1	1		Pakistan
				1	1	1		xxvi	Akyab
				1	1			1 xxvi	Akyab
				1	1			1 xxvii	Akyab
				1		1		1 xxvi	Akyab
				1		1		1 xxvii	Akyab
					1	1	1	xxvii	Akyab
					1	1		1	Akyab
					1		1		Pakistan
					3		3	3 xxvii	Akyab
Specimens	2	10	16	15	20	11	9	10	

Table 8

Location of genital markings in *D. nepalensis* f. *abscisa*

Segment	Intrasegmental position	Localities N	T	Kd	Kw	L
vi	Postsetal, centered at *B*				1	
vii	Setal annulus, in *BC*				1	
	Postsetal, lateral half of *AA*		1			
	Postsetal, in *BC*			1	2	
viii	Presetal, in *BC*			1		
	Setal annulus, lateral half of *AA*		1			
	Postsetal, lateral half of *AA*				1	
	Postsetal, centered at *B*			1		
	Postsetal, in *BC*				3	
ix	Presetal, centered at *B*	2				
	Presetal, in *BC*	4				2
	Presetal, lateral half of *AA*		1			
	Presetal, median	1				
	Setal annulus, lateral half of *AA*		1			
	Postsetal, lateral half of *AA*		2			
x	Presetal, lateral half of *AA*		1			
	Setal annulus, lateral half of *AA*		1			
	Postsetal, median	1	1			
xi	Presetal, centered at *B*		1	1		
	Presetal, in *BC*		1			
	Setal annulus, in *BC*		2			

Localities: N = Nawnghkai, T = Hting bai, Kd = Kadranyang, Kw = Kawapang, L = Lashio.
Existence of usual two secondary furrows is assumed even if furrows are unrecognizable.

Table 9

Frequency distribution of segmental position and number of gizzards in *D. nepalensis* f. *abscisa*

Locality	Segments xiii	xiv	xv	xvi	xvii	xviii	xix	Number of gizzards 3	4	5
Lashio (2)	2	2	2	2	2					2
Tingpai (7)	1	2	7	7	6	5	2	1	3	3
Kadranyang (2)	1	2	2	2	2	1			2	
Nawangkai (14)		12	14	14	14	7			9	5
Kawapang (5)		1	5	5	5	2		2	3	
Totals	4	19	30	30	30	15	2	3	17	10

Drawida papillifer Stephenson 1917
Drawida papillifer papillifer

Ramree (Kyaukpyu), nearby hills, September, 0-5-0. I. M. Ismailjee.
Akyab, September, 0-5-0. I. M. Ismailjee.
Kyauktaw (Akyab), September, 51 juvenile and aclitellate specimens. I. M. Ismailjee.
Buthidaung-Maungdaw (Akyab), September, 0-4-0. I. M. Ismailjee.
Paletwa (Arakan Hill Tract), September, 29 juvenile and aclitellate specimens. I. M. Ismailjee.

External characteristics. Nephropores, present from iii and in x, slightly dorsal to *D* in iii-vii and somewhat more so in viii, occasionally also in ix.

Spermatheeal pores, transverse slits, exactly on or rarely just anterior to 7/8, slightly median to *C*. Male pores, longitudinal or diagonal, in x though but slightly in front of 10/11, at or just lateral to *B*, each usually in a semicircular, indistinctly delimited, whitened area with base at 10/11; occasionally a short transverse furrow just in front of the male pore provides an anterior boundary. Female pores, at *B*, just behind 11/12, in very slight transversely slit-like crevices.

Genital markings, small areas of greyish translucence, circular or shortly elliptical (and then transverse), with very slightly raised and narrow, opaque rims. Markings are located as follows: One, on posterior margin of x immediately lateral to the male pore (5 specimens from Akyab, 16 from Kyauktaw, 9 from Paletwa). As before, but just in front a second marking (20 Kyauktaw, 10 Paletwa). A third marking on posterior margin of x and just lateral to the last of the other two (1, Paletwa). One marking just anterior to male pore (11, Paletwa). One marking in setal annulus of x just lateral to *B* (3 Kyauktaw, 1 Paletwa). One marking on anterior margin of xi, on each side, centered in *AB* or at *B* (5 Akyab). A presetal median marking on xii (1 Paletwa). Other markings are transversely elliptical. One on vii just in front of each spermathecal pore (5 Akyab, 48 Kyauktaw, 22 Paletwa). One in viii just behind each spermathecal pore (4 Akyab, 46 Kyauktaw, 13 Paletwa). One in *AB* of vii, just behind equator on each side (5 Akyab). Presetal, on each side of vii in median part of *BC* (20 Kyauktaw) or centered at m*BC* (11 Kyauktaw), or in lateral half of *BC* (12 Kyauktaw). One in median half of *BC* in setal annulus of vii on each side (4 Kyauktaw). One postsetal on each side of vii in median half of *BC* (5 Paletwa) or in lateral half of *BC* (1

Paletwa) or even dorsal to *D* (13 Paletwa). One in setal annulus of vii, on each side, dorsal to *D* (2 Paletwa).

Internal anatomy. Pigment, present in circular musculature of dorsum even when a bluish color is unrecognizable or almost so externally.

Low longitudinal or vertical ridges are present on inner wall of a postgizzard portion of the esophagus. Gizzards and intestinal origin, respectively, are located as follows: xiii-xv and xxii (1 specimen), xiv-xvi and xxiii (10), xiv-xvii and xxiii (2) or just behnd 23/24 (7), xv-xvi and just behind 23/24 or in xxiv (2), xv-xvii and xxiv (3), xv-xviii and xxiv (2), xvi-xvii and xxiv (3). Commissures from extra-esophageals, anterior to 8/9. From one of the posterior commissures (behind 9/10) a vessel usually passes back into xii or xiii along the dorsolateral aspect of the gut. This vessel often is close to the median plane and when distended with blood probably has been mistaken in the past for a supra-esophageal trunk. A corresponding vessel on the opposite side, in the present worms, may have been empty and hence unrecognizable. Nephridia are present in x.

One testis sac is displaced posteriorly into xii or even farther back in 59 specimens (juvenile, sexual and postsexual). Both sacs are displaced in 1 sexual specimen. Neither is displaced in 9 juveniles, 13 sexual and postsexual specimens. Vas deferens, short, probably about five and certainly no more than ten mm. long. The ental portion runs ventrally within or bound to 9/10, passes in front of heart of ix and then back into x where its short loops are in a small cluster against posterior face of 9/10 well above parietes. Prostates, erect, close to 9/10 so that the vas does not drop to or even very near the parietes though entering the gland below its ental end. Prostates, club-shaped, narrowed ectally, 2-3 mm. long (coelomic portion), capsule rather slender ectally, an entalmost portion of varying length slightly widened and almost spheroidal, shortly ovoidal, or rarely almost ellipsoidal.

Spermathecal atria, in vii, 2-3 mm. long. An ectal portion of variable length, rather slender and duct-like, may be fairly sharply marked off from the widened ental portion. The latter which may be of about the same length as, shorter or longer than the duct is slightly flattened and shortly or elongately elliptical to oval in outline. Whitish, sticky material within the ental portion of an atrium can be disentangled into a long cord. A slight iridescence (spermatozoal?) characterizes cords of one

worm. The coagulum in the spermathecal ampulla is not cord-like and though soft is teased apart only with some effort. Spermathecal duct, slightly widened just prior to passing through 7/8, length and thickness of widened portion slightly variable. Segment xi always open in pinned out worms (82) and the ovarian chamber appears not to be closed off peripherally.

Abnormality. (No. 2) Male pore and associated genital markings of left side lacking. Left spermathecal pore, at 8/9. Left testis sac, vas deferens and prostate, lacking (Paletwa).

Remarks. Distinguished from *peguana* mainly by the male pore locations.

Ramree worms and three from Kyauktaw are slightly different from other west Burma specimens and are briefly characterized below.

External characteristics. Spermathecal pores, apparently just behind 7/8. Male pores, nearer m*BC* than *B*. Female pores, slightly lateral to *B*.

A transversely elliptical (to almost circular) genital marking just median to each male pore, centered at or slightly lateral to *B* and reaching *A*, is larger than other markings of x in these and all other specimens. Small translucent spots, just anterior and posterior or posterolateral to each male pore may be rudimentary markings. Transversely elliptical markings located as follows: one just in front of each spermathecal pore (3 Kyauktaw, 4 Ramree); two in front of each spermathecal pore in a longitudinal series (2 Kyauktaw); one just behind each spermathecal pore (4 Ramree).

Internal anatomy. Gizzards in xv-xvii (3 Kyauktaw). Intestinal origin in xxiii (3).

Testis sacs, not displaced. Vas deferens probably shorter than in other worms as the cluster of loops on the posterior face of 9/10 definitely is smaller. Prostatic duct (portion of capsule without glandular investment), slightly longer.

Coagulum in spermathecal atria, with a slight iridescence, apparently not in a long coiled cord. Atrial stalk, much shorter than the ental sac.

GM gland median to male, enlarged and interrupting longitudinal musculature.

Drawida papillifer peguana Gates 1925

Migyaunglaung (Tavoy), plains, September, 0-5-0. W. D. Sutton.
Pyinthadaw (Tavoy), hills, September, 0-0-1. W. D. Sutton.

Kawlet chaung (Tavoy), nearby hills, September, 0-1-1. W. D. Sutton.
Siyigyan (Tavoy), September, 0-0-6. W. D. Sutton.
Kyaikmaraw (Amherst), August, 0-0-1. K. John.
Thaton, September, 0-26-8. K. John.
Duyinzeik (Thaton), September, 0-14-8. K. John.
Naunggala (Thaton), September, 0-38-15. K. John.
Bilin (Thaton), September, 0-5-6. K. John.
Aungsein (Thaton), September, 0-6-2. K. John.
Sittang (Thaton), October, 0-3-0. K. John.
Boyagyi (Thaton), September, 0-7-0. K. John.
Kyaikto (Thaton), September, 0-12-5. K. John. Nearby hills, 0-9 8. K. John.
Kyaiktiyo (Thaton), September, 0-2-0. K. John.
Taungzun (Thaton), September, 0-45-30. K. John.
Kinmunsakhan (Thaton), September, 0-3-7. K. John.
Kyauktan (Hanthawaddy), August, 0-16-0. K. John.
Syriam (Hanthawaddy), August, 0-2-0. K. John.
Twante (Hanthawaddy), September, 0-10-0. K. John.
Kungyangone (Hanthawaddy), September, 0-7-0. K. John.
Thongwa (Hanthawaddy), August, 3-0-0. Saw San Thwe.
Dedaye (Pyapon), September, 0-1-0. Maung Ohn Maung.
Maubin, October, 0-1-0. Maung Ohn Maung.
Danubyu (Maubin), October, 0-0-1. Maung Ohn Maung.
Wanetchaung (Insein), September, 0-6-0. K. John.
Taikkyi (Insein), September, 0-4-0. K. John.
Dam site (Insein), September, 0-5-1. K. John.
Pegu, August, 0-6-1. K. John.
Henzada, October, 0-1-0. Maung Ohn Maung.
Ingabu (Henzada), October, 0-1-1. Maung Ohn Maung.
Prome, September, 0-4-0. K. John.
Labu (Prome), September, 0-28-6. K. John.
Paukkaung (Prome), September, 0-23-2. K. John.
Pegu Yomas, from 10 miles south of Pyu, September, 0-0-5. G. E. Blackwell.
Pegu Yomas, from 15 miles south of Pyu (Pegu), September, 0-10-3. G. E. Blackwell.
Pegu Yomas, from 32 miles south of Toungoo (Toungoo), September, 0-0-1. G. E. Blackwell.
Pegu Yomas, from 24 miles south of Toungoo (Toungoo), September, 0-2-2. G. E. Blackwell.
Pegu Yomas, from 8 miles south of Toungoo (Toungoo), September, 0-1-0. G. E. Blackwell.
Toungoo, October, 0-5-0. K. John.
Kyaukkyi (Toungoo), October, 0-1-0. Saw Marshall Thwin.
Sah Der, Karen Hills (Toungoo), September, 0-1-0. H. I. Marshall.
Thayetmyo, September, 0-29-7. K. John.
Thanbula (Thayetmyo), September, 0-12-2. K. John.
Magwe, August, 0-10-16. K. John.

External characteristics. Size, of smallest, complete and clitellate specimen, 50 by 3 mm. Nephropores, present from iii, one or both of viii usually dorsal, rarely so in ix and then nearer *D* than in viii, apparently always present in x. An equatorial circle of tiny white spots is present in each segment from iii posteriorly.

Spermatheeal and male pores, larger than female apertures and nephropores, have, in contrast to many other species of *Drawida,* smooth margins and a definite shape.

A whitened area just in front of and just behind each spermathecal and male pore (in x and xi from or just lateral to *B* to or just beyond m*BC*) is present on every specimen and has a definite boundary though not as a rule marked off by a furrow. The epidermis of those areas certainly is not thickened and may be slightly thinned. Genital markings always are present in the whitened areas. Additional markings may be present elsewhere (Table 10).

Internal anatomy. Pigment, in the circular muscle layer, lacking underneath white areas near male and spermathecal pores but present elsewhere in clitellar segments even though unrecognizable externally. Red clitellar coloration, as in other drawidas, in the epidermis.

Esophagus unusually short in the segment behind the last gizzard (as in most drawidas) and thence posteriorly wide, with thick wall bearing internally shortly papilliform to squarish protuberances, closely crowded in longitudinal or vertical rows. The vascular plexus appears in cross sections as a thick, dark red, uninterrupted layer. Valve, narrow, in hinder portion of xxi, anteriorly or posteriorly in xxii. In cross sections the plexus is represented by tiny red dots. In sections through the proximal portion of the intestine the red spots are larger and more closely crowded. Gizzards and valves, respectively, of eleven Rangoon worms are located as follows: xiv-xv and xxi-xxii (1, intestinal origin slightly behind 21/22); xiv-xvi, xxi (3, intestinal origin at 21/22 apparently); xiv-xvi, xxi-xxii (3, intestine beginning midsegmentally or posteriorly in xxii); xv-xvi (2, intestine beginning with 21/22 or midsegmentally in xxii); xv-xvii (2, intestine apparently beginning with 22/23). Commissures from extra-esophageals, in front of 8/9. Nephridia, present in x.

Vas deferens, very short, slightly sinuous in 9/10, looped around heart of ix and extra-esophageal trunk, almost straight in x, not especially thickened ectally. Prostates, 3-5 mm. long.

Spermathecal atria, 2-3 mm. long, ental half (approximately) widened, digitiform, ovoidal or ellipsoidal, abruptly marked off from stalk or more gradually narrowed in an ectal portion. Stalk wall thick, lumen narrow, more irregular entally.

Regeneration. Tail regenerate, 6 mm, long and with 40+ segments, at 65/66. Substrate length, 22 mm.

Remarks. Supposed variation in position of spermathecal pores relative to 7/8 is slight and may be fictitious, e.g., due to slight eversion from the spermathecal duct.

Intestinal origin was determined in Rangoon worms that had been anesthetized, pinned down straight, and then fixed. The esophagus was almost straight. Records of gizzard locations in worms listed above no longer are available.

TABLE 10

Location of genital markings in *D. papillifer peguana*

	Segments					
	vii	viii	viii	ix	vii	viii
		paired			median	
Locality	presetal		postsetal			
Naunggala (51)	6	9				
Taungzun (45)	7	14		3		
Kyauktan (14)	5					
Paukkaung (23)	10	6			2	
Thaton (32)	7	6				1
Wanetchaung (6)	6	2				
Magwe (26)						
Toungoo (4)					2	
Dam site (4)						
Ingabu (2)						
Labu (32)					5	
Kinmunsakhan (10)		1				
Pegu (4)				1		
Bilin (21)						
Pegu Yomas (22)		8		4	1	
Duyinzeik (22)	3	2				
Kungyangone (7)						
Twante (5)	1			2		
Kyaikto (13)		1				
Aungsaing (7)	1					
Tavoy district (12)			2			

Drawida rangoonensis Gates 1925

Sittang (Thaton), October, 0-1-3. K. John.
Kyauktan (Hanthawaddy), August, 0-0-2. K. John.
Rangoon (Hanthawaddy), various dates, 0-5-21. K. John.
Twante (Hanthawaddy), September, 0-7-9. K. John.
Pyapon, September, 0-2-1. Maung Ohn Maung.
Kyaiklat (Pyapon), September, 0-1-4. Maung Ohn Maung.
Maubin, October, 0-1-3. Maung Ohn Maung.
Bassein, October, 0-0-3. K. John.
Pegu, jungle to the east, August, 0-0-2. K. John.
Myohaung (Mandalay), September, 0-0-14. K. John.
Bhamo, September, 0-3-14. K. John.
Myitkyina, September, 0-7-3. K. John.

External characteristics. Nephropores, present from iii, in viii-ix usually slightly dorsal to *D*, apparently lacking in x. Clitellar coloration, sometimes lacking in *AA* of x-xi and more rarely of xii.

Spermathecal pores, very small transverse slits exactly on 7/8, margins usually smooth but not as straight as in *peguana*. Male pores, very small transverse slits, just in front of or more definitely anterior to 10/11, margins almost always slightly tumescent and often with an appearance of a thickly annular lip.

A transverse, slightly depressed, translucent area on each side of x is in the median half of *BC* and the equivalent of a setal annulus (secondary furrows lacking). The epidermis between that area and 10/11 is whitened and rarely with a diagonal or longitudinal central area of greyish translucence. Other paired genital markings usually are longitudinal but on viii and ix may be almost circular or more rarely transverse, in a middle or lateral portion of *BC* of x just lateral to translucent area, similarly positioned in ix but in viii more lateral and often just median to *C*, in viii-ix often in equivalents of setal annuli, in x-xi extending across equivalents of presetal and setal annuli and often reaching farther posteriorly, occasionally even to posterior intersegmental furrow. Median markings, usually between an intersegmental furrow and the equator, reach laterally to *A*, *B* or into *BC*. All markings except those in setal annulus of x are areas of slight epidermal thickening but without clitellar coloration.

Internal anatomy. Gizzards, 2-4, in xii-xvii (Table 12). Esophagus behind gizzards, usually distended by ingesta, rather sigmoid, on the floor at mV one or two longitudinal lamelliform ridges, or a horizontal band marked off into 2-4 sections. The

vascular plexus is much thicker, except just behind last gizzard and in the valve, than in the intestine. Gizzards and intestinal origin, respectively, of Rangoon specimens: xiii-xv, immediately behind 22/23 (3); xiv-xvi, midsegmentally in xxiii (1) or immediately behind 23/24 (5); xv-xvii, immediately behind 24/25 (1).

Commissures from extra-esophageals, in front of 8/9. The hearts of viii unite above the esophagus to open into dorsal trunk through a single short vertical vessel in median plane. Nephridia, of x lacking (10 adults).

Vas deferens, slender and iridescent entally, passing ventrally median to the heart and then looped around the heart of ix, after passing into x in several hairpin loops (not always easy to find), then thickened and in a cluster of loops that may be nearly as large as or larger than the testis sac. Prostates, 1.0-1.5 mm. long, capsule slightly widened entally.

Spermathecal atria, 3-5 mm. long, saccular rather pear-shaped. A short ental portion of the sac occasionally is invaginated into the atrial lumen. Spermatozoal iridescence, slight, has been noted (several specimens) in atria as well as ampullae.

Remarks. Nephropores of ix and xi often are difficult to identify though probable sites are recognizable even when patent apertures were not seen. A more or less pore-like marking occasionally visible near *D* of x presumably marks site of a nephropore that was functional in juveniles stages.

TABLE 11

Location of genital markings in *D. rangoonensis*

	Segments								
	viii	ix	x	xi	viii	ix	x	xii	xiii
Locality	Paired				Median				
Rangoon	26	26	26	26		1		1	25
Kyauktan	2	2	2	2			2		2
Pyapon	2	2	3	3				1	2
Myohaung	6	6	14	14	3			1	13
Kyaiklat	4	4	5	5	1				5
Pegu			2	2	1				2
Bassein	3	3	3	3			1		1
Maubin	4	4	4	4					4
Twante	11	13	16	16			2	3	13
Sittang	2	3	3	3				3	1

Median markings of viii-ix and xii-xiii are postsetal, but in x are presetal. Paired markings are in *BC*.

TABLE 12

Frequency distribution of segmental position and number of gizzards in *D. rangoonensis*

Locality	Segments						Number of gizzards		
	xii	xiii	xiv	xv	xvi	xvii	2	3	4
Twante (6)	1	4	5	6	3	1		4	2
Maubin (4)		3	4	4			1	3	
Pyapon (3)		3	3	3				3	
Kyaiklat (2)		2	2	2				2	
Sittang (1)		1	1	1				1	
Kyauktan (2)		2	2	2	1			1	1
Bassein (3)		1	3	3	3	1		1	2
Rangoon (14)		8	13	14	12	1	1	6	7
Totals	1	24	33	35	19	3	2	21	12

DRAWIDA RARA Gates 1925

Kamaungthwe River (Tavoy), September, 0-2-0. W. D. Sutton.
Moulmein (Amherst), August, 0-3-6. October, 0-2-1. K. John.
Mupun (Amherst), October, 0-26-18. K. John.
Thaton, September, 0-14-20. K. John.
Duyinzeik (Thaton), September, 0-7-0. K. John.
Naunggala (Thaton), September, 0-0-3. K. John.
Bilin (Thaton), September, 0-4-0. K. John.
Aungsaing (Thaton), September, 0-8-5. K. John.
Sittang (Thaton), October, 0-13-1. K. John.
Syriam (Hanthawaddy), September, 0-9-5. K. John.
Rangoon (Hanthawaddy), various dates, 0-39-36. K. John.
Kungyangone (Hanthawaddy), September, 0-2-0. K. John.
Dedaye (Pyapon), September, 0-1-0. Maung Ohn Maung.
Bassein, October, 0-15-18. K. John.
Danubyu (Maubin), October, 0-2-0. Maung Ohn Maung.
Hlawga (Insein), September, 0-3-0. K. John.
Taukkyan (Insein), September, 0-3-1. K. John.
Hmawbi (Insein), September, 0-10-5. K. John.
Wanetchaung (Insein), September, 0-18-3. K. John.
Taikkyi (Insein), September, 0-23-14. K. John.
Dam Site (Insein), September, 0-44-2. K. John.
Pegu, August, 0-16-10. Jungle to the west, 0-14-4. Jungle to the east, 0-13-10. K. John.
Thayetmyo, September, 0-2-0. K. John.
Allanmyo (Thayetmyo), September, 0-2-0. K. John.
Pyinmana (Yamethin), October, 0-8-0. K. John.
Taungdwingyi (Magwe), August, 0-23-18. K. John.
Magwe, August, 0-4-6. K. John.
Minbu, August, 0-2-2. K. John.
Myohaung (Mandalay), September, 0-1-4. K. John.

Wuntho (Katha), hills to the west, September, 0-0-1. Saw San Thwe. Myitkyina, September, 0-18-14. K. John.

External characteristics. Length, 35-50 mm. (Taungdwingyi, Aungsaing and Magwe). Nephropores, present from iii, close to *D* in viii-ix, apparently always lacking in x. Clitellar coloration, red, often lacking ventrally in x and a presetal portion or all of xi, the uncolored area often delimited by slightly irregular longitudinal furrows at level of lateral margins of male porophores.

Spermathecal and male pores, larger than nephropores and certainly larger than female apertures, transversely slit-like. Spermathecal pores, at or just median to *C*, each usually surrounded by an annular lip, the pore apparently located on posterior margin of vii, the lip when specially swollen with an appearance of a short transverse papilla. Rarely, a posterior portion or even all of the lip is lacking and then the pore appears to be on 7/8. The tumescence is believed to be an everted portion of the spermathecal duct.

Genital markings: paired and nearly circular, pre- and postsetal in *BC* of x, transverse and in setal annuli of x and xi just lateral to *B;* unpaired, presetal and postsetal in *BB* (or reaching slightly into *BC*) of viii, x-xi. Markings in setal annuli often are slightly smaller than other paired markings, greyish translucent rather than white, depressed rather than protuberant and without epidermal thickening. Paired markings occasionally present in *BC* of viii (pre- and postsetal) or vii (postsetal) are transverse, indistinctly demarcated areas of epidermal thickening. Paired postsetal markings usually (Pyinmana, Taungdwingyi, Minbu, Magwe, Allanmyo, Thatyetmyo) are lacking in x.

Internal anatomy. Gizzards, 2-4, in xii-xviii (Table 13). A midventral, typhlosole-like ridge is present in the gut behind the gizzards but may not be as obvious as in *rangoonensis*. Location of gizzards and intestinal origin, respectively, in several Rangoon specimens: xiv-xvi, midsegmentally in xxii (3) or just behind 22/23 (2); xv-xvii, just behind 22/23 (4) or midsegmentally in xxiii (12) or just in front of 23/24 (1) or just behind 23/24 (2); xv-xviii, midsegmentally in xxiii (2); xvi-xvii, just behind 22/23 (1) or midsegmentally in xxiii (1) or just behind 23/24 (2); xvi-xviii, just in front of 23/24 (1) or just behind 23/24 (6). The intestine begins, in a Taungdwingyi worm with gizzards in xiv-xvi, just behind 21/22. Commissures from extra-esophageals, in front of 8/9.

Vas deferens, short, slender, with several loops in 9/10 and on anterior face of 9/10, twisted around hearts of ix, with several further loops on posterior face of 9/10 in a small compact cluster, an ectal portion only slightly thickened.

Abnormality. (No. 1.) Right spermathecal duct, about half way down to parietes, passes into vii where a short portion is widened into a thin-walled vesicle. (No. 2.) Right male porophore entirely in x and extending from the presetal secondary furrow nearly to 10/11. The male pore is about midway between eq/x and 10/11. (No. 3.) Testis sac, vas deferens, prostate, male pore and porophore as well as genital markings of left side, lacking.

Regeneration. Tail regenerates, of 28+ segments at 72/73 and of 26+ segments at 81/82. Lengths of substrates and regenerates, respectively, 28 and 4, 31 and 5 mm.

Remarks. Male porophores of four Taikkyi worms are represented only by circular areas of epidermal whitening, distinctly demarcated but not protuberant. The pores are transversely placed slits at 10/11 which appear to be nearly as deep across the porophore as elsewhere. Prostates of these specimens are unusually high in the coelomic cavity though capsules still are almost confined to the parietes.

Male porophores in *rara* seem incapable of marked elevation. However, by bringing the prostatic capsule deeper into the parietes, a small part of the porophore containing the male aperture can be raised into a teat-like protuberance presumably for insertion into the spermathecal pore. The lumen in the thickened portion of the spermathecal duct may be large enough to receive the protuberance. Entrance perhaps is facilitated by slight eversion of the duct.

The unusually small size of the prostatic capsule presumably is secondary rather than primitive but in either case distinguishes *rara* from *constricta* Gates 1929. Connectives from the extra-esophageal trunks are on opposite sides of septum 8/9 in the two species. Discoidal male porophores extending into x and xi have been developed in both species but seem capable of greater elevation (as temporary intromittent organs) in *constricta*. Genital markings of both species are similar to those of *spissata* Gates 1930 where they also are not associated with definite glands. The male pores of *spissata* certainly do appear to be well inside xi but all specimens had protruded porophores (discoidal on relaxation and restricted to xi?). Assuming that adiverticulate

spermathecae are evidence, in Burma, of phylogenetic relationships, *spissata* can be derived from a common ancestor of *rara* and *constricta* by the following changes: migration of male pores back into xi, increase in number of gizzards (now apparently 4-5), elongation of esophagus so as to place the gizzards farther posteriorly, elongation of prostates as well as male deferent and spermatheeal ducts. Additionally, the spermatheeal ducts have been thickly muscularized, especially so in the ectal 35-50 mm., and the vasa deferentia (in x only) have been thickened.

TABLE 13

Frequency distribution of segmental position and number of gizzards in *D. rara*

Locality	Segments							Number of gizzards		
	xii	xiii	xiv	xv	xvi	xvii	xviii	2	3	4
Magwe (15)	1	12	15	15	9				8	7
Wuntho (2)		1	1	2	2			1		1
Taungdwingyi (6)		1	5	6	4			2	4	
Thaton (11)		1	11	11	11	8			2	9
Pegu (22)		6	17	22	22	14	2		5	17
Mupun (15)		2	12	15	15	10	2		4	11
Myohaung (5)			4	5	5	1			5	
Taikkyi (5)			4	5	5	1	1		4	1
Rangoon (9)			1	9	9	6	2	2	5	2
Bassein (2)				2	2	2	2			2
Syriam (2)				2	2	2	2			2
Totals	1	23	70	94	86	44	11	5	37	52

DRAWIDA TENELLULA nom. nov.

1933. *Drawida* sp., Gates, Rec. Indian Mus., 35:476.

Remarks. Ovisacs were small in both specimens (aclitellate) but other genital organs probably were fully developed.

The "penes," if definite structures, presumably are retractile into chambers possibly restricted to the parietes. Otherwise, the penes could be produced perhaps by eversion of the prostatic duct. In either case complete retraction is likely to leave a fairly large secondary male pore that would provide an additional distinction from the various species mentioned below. Protrusion of a discoidal porophore in a tubular fashion now seems unlikely and is contra-indicated by texture of penial epidermis.

D. tenellula is distinguishable from *bullata* by the penis-like male porophores and absence of definite genital markings. From

other species with shortly digitiform spermathecal atria *D. tenellula* is further distinguished as follows. From *D. vulgaris* by the longer vas deferens. From *D. gracilis* by the much smaller size, smaller ventral setae of iii-vii, erect prostates, thickening of the vas in xi, peripheral closure of ovarian chamber. From *D. flexa* by the longer vasa deferentia and absence of special parietal glands associated with genital markings.

Drawida victoriana n. sp.

Mount Victoria (Pakokku Chin Hills), on east side near path from Kanpetlet to summit, at 3000 feet, in teak forest and grass land, July, 0-1-0. G. Heinrich.

External characteristics. Length, 64 mm. Diameter, 3 mm. Setae, unrecognizable or almost so in an anterior portion of the body, posteriorly $AA < BC$, AB slightly $< CD$. Nephropores, present from iii, at or close to *D.*

Spermathecal apertures, probably at 7/8 and at or just median to C. Male pores, in x and very slightly lateral to *B*, very small, transverse slits at tips of anteriorly directed, rather conical protuberances from posterior margin of x. Porophores are in slight depressions where the epidermis is whitened, smooth and glistening.

Genital markings, small, median and postsetal in vii-xi, paired, in BC and about in line with male porophores, in presetal and also in setal annulus of x, in postsetal annulus of xi. A smaller presetal marking is present in lateral portion of *AA* in x. Each marking, except in vii, nearly circular, with a distinctly demarcated rim and a longitudinal or transverse area of greyish translucence centrally.

Internal anatomy. Septa, 5/6-8/9 muscular. Gizzards, four, in xvi-xix. Commissures from extra-esophageals, in front of 8/9.

Testis sacs, dislocated posteriorly behind the ovarian chamber. Vas deferens, slender and iridescent entally in 9/10 and in ix near hearts, a preseptal portion in ix 5-10 mm. long and in a small cluster of u-shaped loops, the postseptal portion thickened and in a cluster of loops that is as large as or larger than the testis sac, passing directly into prostate just below its ental end. Prostates, rather slenderly club-shaped, 2½ mm. long, nearly straight or bent into a u-shape, capsule slenderly club-shaped and nearly circular in cross section.

Spermathecal duct, slender, slightly zig-zag looped as it passes ectally on posterior face of 7/8. Atrium, saccular, large, erect in vii and in contact with dorsal parietes, the ectal half stalk-like. Annular ridges are present on inner wall of stalk and sac. Ovarian chamber, probably closed off from parietes. Ovisacs, in xii-xiv or xv.

Longitudinal musculature, uninterrupted over sites of genital markings.

Remarks. Pigment was not recognized and may be lacking but the body wall had been deeply stained by some post-mortem accident. The anterior end was distorted probably as a result of local desiccation.

Yolk was present only in a posterior portion of partially collapsed ovisacs, a condition that is suggestive of an early post-sexual stage. The glandular investment of the prostates, thin and firmly adherent to the capsule, is more like conditions of a presexual stage.

Genital markings of the kind present on the type, in other species usually are associated with small solid glands having transparent walls. If such glands are present, *victoriana* is distinguished from *papillifer* and *nagana* by the protuberance of the male porophores and from *nepalensis* by location of male pores in x as well as by characters of the porophores. If glands are absent, *victoriana* is distinguished from *rangoonensis* by the protrusibility of the male porophores and from *molesta* by absence of penes. To permit entry in a key, glands are assumed to be present.

Reproduction. Iridescence in an ental portion of the male gonoducts shows that sperm had been matured. A similar iridescence in the coagulum of an ectal portion of the atrial stalk shows that sperm had been received, presumably from another worm. Reproduction, accordingly, is assumed to be sexual and biparental. (No iridescence was recognizable in the coagulum within the spermathecal ampulla.)

Regeneration. A tail regenerate is 3 mm. long.

Drawida vulgaris Gates 1930

Prome, September, 0-2-12. K. John.
Paukkaung (Prome), September, 0-18-20. K. John.
Mt. Popa (Myingyan), September, 0-0-2. K. John.

External characteristics. Length, to 50 mm. Diameter, 2½-3 mm. Nephropores, present from iii, in or close to *CD*, apparently

lacking in x. Setae, *AA* usually < *BC* but on some Paukkaung worms may = *BC*, *DD* ca. = ½C.

Male pores, small transverse slits on posterior margin of x, at or slightly median to m*BC*, with or without an obvious though small, annular lip. A posterior portion of x bearing the male pore may be protuberant as on the types or not. In the latter case the male pore is concealed from view by the anterior margin of xi.

Genital markings, transverse, shortly elliptical, presetal, opaque areas, each with a greyish translucent center, in Paukkaung worms indistinctly delimited and recognizable only in best optical conditions. Paired markings usually are in a lateral portion of *BC*, with centers slightly lateral to levels of male pores. A pair of whitened patches usually slightly nearer *B* on each of the present worms extends from 10/11 to postsetal secondary furrow of x. In one or the other of those patches there occasionally is recognizable a typical marking with central translucence. Markings apparently are lacking on the Popa worms. The markings of Paukkaung and Prome worms, respectively, are as follows: in ix (38 and 12 specimens), in x (38 and 12); median, in *AA*, of viii (1 and 5); of ix (17 and 9); of x (0 and 4); of xi (19 and 7); of xii (14 and 6); of xiii (1 and 0).

Internal anatomy. Gizzards, two to four in xii-xvi, xii-xiv (3 Prome), xii-xv (1 Paukkaung), xiii-xiv (1 Paukkaung, 2 Prome), xiii-xv (4 Paukkaung, 2 Prome), xiv-xvi (1 Popa). Commissures from extra-esophageals, in front of 8/9. Posterior commissures from extra-esophageals pass into hearts of ix just lateral to median plane. Hearts of ix unite mesially just above gut and are then connected with the dorsal trunk by a short, vertical vessel in the median plane. A vessel from the posterior commissures of the extra-esophageals passes posteriorly on dorsolateral face of the gut to xii or xi. Nephridia of x, lacking.

Testis sacs, usually laterally flattened, equally in ix and x, rather reniform to shortly u-shaped, concave ventrally, more or less deeply constricted by 9/10. Vas deferens, slender and iridescent entally, passing into ix median to the heart, then anterior to the heart and back to 9/10 where it is twisted into several short loops, the portion in x thickened and opaque, also twisted into several loops, then passing directly into the prostate. The vas of one Prome worm is about 8 mm. long, length of the slender portion just over 3 mm. Prostatic capsule, about one mm. long, slenderly rod-like but with some slight ental widening,

soft, opaque, of about the same thickness as the glandular investment.

Spermathecal atria, always in vii, about one mm. long.

Remarks. Differences from *bullata* are few but apparently constant in a range that extends into Thailand. Vasa deferentia of all specimens referred to *vulgaris*, like the spermathecal atria, have been short as in the smallest specimens of *bullata*. Male pores of *bullata* always were in or appeared to be in xi. In *vulgaris*, however, the male pores always were in or appeared to be in x.

TABLE 14

Location of genital markings in *D. vulgaris*

Locality	Segments							
	ix	x	viii	ix	x	xi	xii	xiii
	Paired				Median			
Paukkaung	38	38	1	17	—	19	14	1
Prome	12	12	5	9	4	7	6	—

Paired markings are located laterally in *BC*. Median markings are confined to *AA*.

TABLE 15

Frequency distribution of segmental position and number of gizzards in *D. vulgaris*

Locality	Segments					Number of gizzards		
	xii	xiii	xiv	xv	xvi	2	3	4
Prome (6)	3	7	7	2		1	4	1
Paukkaung (7)	1	6	6	5		2	5	
Mt. Popa (1)			1	1	1		1	
Totals	4	13	14	8	1	3	10	1

Genus MONILIGASTER Perrier 1872

MONILIGASTER CERNOSVITOVI nom. nov.

1940. *Moniligaster beddardi* Gates, Rec. Indian Mus., 42:496. (Type locality, Kodaikanal. Types in the Indian Mus.)

M. beddardi Gates 1940 is preoccupied by *M. beddardii* Rosa 1890 now *Drawida beddardi*, and would have been renamed long ago had there been any occasion to refer to the genus.

MONILIGASTRID PHYLOGENY

The numerous differences from most earthworms suggest long separation of moniligastrid stocks from other lines of megadrile

evolution. Unless peculiar characteristics, in identical combinations, evolved independently in the ancestry of each genus, an early moniligastrid should have differed from contemporaneous oligochaetes as follows: prostomium, now independent of the peristomium and attached to the roof of the buccal cavity behind level of intersegmental furrow 1/2; digestive system, with enterosegmental organs, with esophagus elongated posteriorly so that the gizzard is behind the ovarian segment, perhaps with intestinal origin at first in xv where it still is today in many megadriles; vaseular system, with paired extra-esophageal trunks that are lateral to the hearts, with a parietal subneural trunk, one or two pairs of hearts at posterior end of the series united dorsomesially in each segment instead of opening into the dorsal vessel directly; testes, proliferating anteriorly into interior of their septa and no longer inducing development of seminal vesicles; ovarian chamber, closed off mesially from neural and esophageal portions of the coelom; spermathecae, deeply invaginated into the coelom so that ampullae are dorsal; capsular genital glands, evolved from the X glands. While so much typieally moniligastrid anatomy was being evolved, gonads of the ancestral battery may well have been eliminated in all but four segments, x-xiv.

Ancestral characters still retained were as follows: genital apertures, of all organs from spermathecae to glands, minute, superficial, in the ventrum; spermathecal, male and female pores in region of *AB;* gland pores variously located in *BB;* sigmoid setae, in four pairs of longitudinal ranks; clitellum, unilayered; gonoducts short, and opening directly to the exterior in presetal portions of the segments; hearts, lateral (a supra-esophageal trunk still lacking); ovisacs, dorsal and posteriorly elongated; gizzard, still esophageal and single; nephridial ducts, passing straight through the parietes. Pigment may have been lacking.

An important early change in moniligastrid anatomy resulted from acquisition by genital glands of ability to attract toward and into themselves during early growth the elongating male gonoducts. At first gonoducts may have joined, regardless of location, the nearest glands, or if several were equidistant those that were growing faster or had invaginated earlier. Eventually stabilization was aehieved and the vasa deferentia joined only those glands developing at the intersegmental level next behind that of the gonad septum. Henceforth, male gonoducts were to be unable to open to the exterior in absence of prostates.

Reduction in the gonad battery was continued. In a line leading to *Desmogaster*, gonads of x were aborted and those of xii became testes. In lines leading to *Hastirogaster* and *Eupolygaster*, gonads of x and xii, of x and xiii, respectively, were eliminated. In the main line leading to *Drawida-Moniligaster*, gonads of xii-xiii disappeared (unless a segment was excalated anteriorly), those of xi being retained as ovaries. Other reductions and modifications in the battery would seem to have been possible. If so, additional genera may be found in unexplored portions of the moniligastrid domain east of Burma.

Development of additional hearts at posterior end of an ancestral series appears to have been limited by location of the ovarian chamber as none have appeared behind a level two segments in front of that chamber. Thus, the last hearts of drawidas are in ix but of desmogasters are in xi. One pair of spermathecae was eliminated in the ancestry of *Drawida* (and *Hastirogaster?*) but elsewhere the reduction has been intrageneric.

Subsequent to appearance of extant genera, known macroscopic changes have been confined almost entirely to short portions of nephridial ducts, a section of the gut behind the ovarian segment and, of course, to the genital system. Parietal portions of nephridial ducts now may grow laterally as well as mesially within the body wall to acquire at several levels external openings, often irregularly placed and with more or less asymmetry. The esophagus has been further elongated. Esophageal gizzards (cf. Tables 16-17) have been multiplied and moved posteriorly. Body size has been increased sufficiently, in various countries, to warrant the characterization of "giant earthworms." These somatic modifications now appear to have been made independently in various genera.

Among independently made changes in the genital system are: lateral dislocations of male and spermathecal pores; closure of the ovarian chamber from the parietes; elongation of spermathecal and male ducts; development of intromittent organs; various modifications in shape of the prostatic capsule as well as reduction (and final elimination?) of the glandular investment.

Female pores have remained in their primitive position throughout the family, and spermathecae still are adiverticulate except in various lineages of *Drawida*. Although more information is available for that genus than for all others it is not yet sufficient to allow more than a tentative indication of relationships and changes in a few small groups.

A rather primitive *willsi* species group has retained prostate-like (GM) glands but has acquired pigment. Spermathecae still are adiverticulate in the Assamese *limella* Gates, 1934, but pores are at m*BC*, gizzards are three in xiii-xv and the prostatic capsule has become so small that it is almost confined to the parietes. Genital apertures still are at or close to *B* in species of peninsular India which now have spermathecal atria. *D. scandens* Rao, 1921, with prostates and GM glands of the same size, has two or three gizzards in xii-xv. *D. dolosa* Gates, 1945, with two to four gizzards in xiii-xvi, has shortened prostates that may be only a quarter as long as the GM glands. *D. periodiosa* Gates, 1934, with two or three gizzards in xiii-xvi has prostatic capsules so small as to be almost confined to the body wall. *D. willsi* Michaelsen, 1907, with two to four gizzards in xii-xvi, has GM glands that are shorter and slenderer than the prostates. Occasional individuals have no glands.

All Burmese species have spermathecal pores at or close to *C* and a region around site of each primary male pore usually is modified to some sort of a porophore for more efficient transfer of sperm during copulation.

A *beddardi* group, probably with a peripherally closed ovarian chamber, lacks pigment and spermathecal diverticula though a terminal portion of the spermathecal duct is thickened. *D. delicata*, with four gizzards in xii-xv, has markedly lengthened male gonoducts but spermathecal ducts still are short. *D. kempi* Stephenson, 1914, with gizzards in xv-xix, has spheroidal prostatic capsules. *D. rara*, with three to five gizzards, in xii-xviii, has prostatic capsules that are vestigial and confined to the parietes. *D. constricta*, probably close to *rara* but with only two or three gizzards in xiv-xviii, has less shortened prostatic capsules that still reach into coelomic cavities. *D. spissata* Gates, 1930, with four or five gizzards in xvii-xxi, has much lengthened prostates, vasa deferentia and spermathecal ducts, the latter markedly muscularized ectally. *D. beddardi*, with three or four gizzards in xii-xix, still has digitiform prostatic capsules but with the glandular investment occasionally restricted to small ental portions. Male pores have been invaginated and now are on tubular penes pendent from roofs of eversible, muscular-walled chambers more or less protuberant into the coelom.

Possibly derived from a distant ancestor of the *beddardi* group is *caerulea*, with pigment, male pores deeply invaginated

into muscular copulatory chambers that have no glandular investment and contain no penes. Spermathecae, in the southern portion of the range, still are adiverticulate though the terminal thickening of the duct may be slightly larger than in the *beddardi* group. A muscularized atrial outgrowth of the thickened portion of the duct has appeared in more northern forms and still farther north has reached septum 6/7 and the dorsal parietes. Elongations already under way in the north have become even greater in the Assamese *decourcyi* with atria, spermathecal and male ducts, respectively, reaching lengths of 8, 20 and 650 mm. Gizzards, still only 1 or 2 in xiii-xvi of a central Burma population, in *decourcyi* now are 7-9 in xiv-xxvii.

Other Burmese species, all with divertieulate spermathecae, appear to belong in two groups of more or less elosely related forms distinguished by presence or absence of definite glands (not prostate-like) in association with the genital markings. One section of the glandless group has digitiform spermathecal atria. Three species still have digitiform prostatic capsules: *D. vulgaris,* with 2-4 gizzards in xii-xvi, short atria and vasa deferentia; *D. tenellula*, with 3-4 gizzards in xiii-xviii, and lengthened vasa; *D. bullata,* with 1-5 gizzards in xiii-xviii, atria and vasa that vary from short to considerably elongated. *D. gracilis*, with 1-4 gizzards in xiv-xxi, short atria, lengthened vasa but prostatic capsules that reaeh into coelom only slightly. *D. lacertosa*, with 3-5 gizzards in xiii-xx, short but muscularized spermathecal ducts and atria, has lengthened vasa, anteroposteriorly elongated and bilobed prostatic capsules sessile on the parietes.

An ental portion of the somewhat elongated spermathecal atria, in the second section of the glandless group, has become a thin-walled sac. *D. rangoonensis*, with 2-4 gizzards in xii-xvii, has elongated vasa but nearly digitiform prostatic capsules. *D. molesta*, with 3-5 gizzards in xiii-xxi, elongated vasa and prostatic capsules, has invaginate male pores on tubular penes.

GM glands of the remaining group are solid and bear on their outer faces part or all of a more or less distinctly delimited genital marking. Most species have digitiform atria. Two of the species in that section have elear glands with transparent or translucent walls. *D. assamensis*, with 4-5 gizzards in xii-xvii, has short spermathecal ducts, atria, vasa deferentia and prostatie capsules. *D. flexa,* in peninsular Burma, also has short atria and vasa but the gizzards (4-5) are in xvi-xxiv and glands are much more numerous. *D. nana,* with 2-3 gizzards in xiii-xv, has

Table 16

Frequency distribution of gizzard number and of segmental position in *Drawida longatria* and closely related species.

Number of gizzards					Locality	Segments									
	26	30			Sagaing	1	19	55	51	16					
	13	42	1		Tonbo-Kyaukkyone	2	23	44	50	31	6				
	43	12	1		Kaungmudaw		1	15	56	49	5				
2	28	18			Thazi		4	15	34	38	21				
	28	33			Mandalay-Tonbo		2	15	40	54	36	8			
		8	2		Maubin			1	6	10	10	5			
	1	12	16	1	Rangoon			6	27	29	26	16	3		
	9	38	5		Bassein-Kokya-Kochi			8	30	48	42	22	2		
	3	8	7		Yamethin			1	9	16	16	13	3		
	1	16	10		Tharrawaddy			1	5	13	26	26	17	2	
		6	107	21	2 Tavoy			8	70	114	136	134	79	21	1
		28	7		Sandoway				8	32	35	31	6		
	1	30	7	1	Pyapon				9	31	39	34	10	2	
		3	5	1	Blachi-Leiktho				2	8	9	9	6		
		3	6	1	Chaungson				2	3	8	10	9	6	
		2	8	1	Shwegyin-Paung						5	9	10	11	7
		6	87	31	*D. tumida* Various				10	77	116	124	119	67	8
		10	80	10	*D. flexa* Various				2	34	80	98	105	87	29

TABLE 17

Frequency distribution of segmental position and of gizzard number in other species of *Drawida*.

Segments										Number of gizzards						Species
12	13	14	15	16	17	18	19	20	21	1	2	3	4	5	6	
18	48	53	39	4							6	38	9			*vulgaris*
26	91	99	50	10							29	66	5			*willsi*
14	77	116	117	64	7						9	71	41			*calebi*
5	54	97	100	70	3						3	65	32			*rangoonensis*
4	50	177	266	255	163	33					5	135	127	5		*rara*
1	5	56	98	98	63	23	4				6	66	32	2		*papillifer peguana*
	13	59	94	71	25	6					52	48	5			*caerulea caerulea*
	6	31	44	44	38	19	2					6	24	14		f. *abscisa*
	1	16	38	49	48	35	7					8	34	6	1	*lacertosa sepulta*
	1	12	58	64	54	26	3	1			9	39	21			*papillifer papillifer*
		8	21	33	41	30	19	4	2	1	10	35	8			*gracilis*
					12	12	12	12	2				10	2		*spissata*

glands with opaque but soft walls. Vasa, atria, possibly spermathecal ducts and prostates, are lengthened. The rest of the species in the section have glands with thickly muscular walls. *D. tumida*, with 3-5 gizzards in xvi-xxii, has short atria but vasa are somewhat elongated. *D. longatria,* with 1-6 gizzards in xiii-xxiii, has spermathecal atria 2-180 mm. long. Male gonoducts are of similar variable lengths.

An ental portion of the somewhat elongated spermathecal atria has become a thin-walled sac in other Burmese species which have almost digitiform prostatic capsules and (one exception?) clear glands. *D. papillifer,* with 2-5 gizzards in xii-xx still has short vasa, no protuberant male porophores and an ovarian chamber that is not closed off from the parietes. Pigment, possibly similar to that of *caerulea*, is present. *D. nepalensis* and *victoriana*, with gizzards in xii-xxiii and xvi-xx, respectively, now have elongated vasa, protrusible male porophores and an ovarian chamber closed off from the parietes.

OLIGOCHAETE PHYLOGENY

The supposedly Jurassic or Cretaceous ancestor of the megadriles usually was believed to be octogonadal, with testes in x-xi and ovaries in xii-xiii. Divergent conditions in modern earthworms, except moniligastrids, resulted from elimination of the anterior ovaries and, less frequently, of the first or second pair of testes. The phylogenetic puzzle posed by the Moniligastridae required answers to several questions among which were the following: 1) How had testes of x-xi gotten into xi-xii during evolution of *Desmogaster* from the supposedly ancestral haplotaxid? 2) How did ovaries of xiii get into xi as *Drawida*[3] was evolving from *Desmogaster?* 3) At the same time, how did one pair of desmogaster testes, either from xi or from xii, get into x? 4) How had male gonoduct funnels gotten from one septum into sacs of the preceding septum?

Evolution of gonadal batteries within the Moniligastridae requires "some possibility of the intercalation or excalation of segments" according to Beddard (1891) who offered no suggestions as to how the deletions or insertions could have been brought about. The only attempt at a solution of the moniligastrid puzzle is Stephenson's ingenious "contraction" theory which Avel

[3] *Drawida* is understood, in most of this discussion, to include *Moniligaster*. The genera are so much alike that Michaelsen seems to have repented separating them. *Moniligaster* may be only an unusually distinct species group.

(1959) deems plausible. Michaelsen, however, appears to have been unwilling to approve — except for mention of several difficulties in a footnote (1922), he continued to ignore the problem which certainly was involved in his own derivation of the Moniligastridae from the Haplotaxidae.

If moniligastrid testis sacs, as Beddard suggested, are vestigial coeloms of segments from which all parts except gonads, gonoducts and their funnels have disappeared, it should be possible to determine the ancestral condition by "expanding" the sacs to their original metameric state. The genera thus theoretically treated by Stephenson are *Syngenodrilus* and *Desmogaster*. Results were identical, testes in xii as well as x and ovaries in xiv (for figures cf. Stephenson, 1922 or 1930). Then, to restore the primitive continuity of the series, testes were inserted in xi and ovaries in xiii thus providing a decagonadal battery. Conditions in most megadriles resulted from elimination of gonads in xiv, xii and x or xi but in moniligastrids resulted from partial or complete abortion of gonad segments. Contraction of the tenth and twelfth segments to testis sacs along with elimination of testes in xi and of ovaries in xiii produced *Desmogaster*. Fusion of desmogaster testis sacs and elimination of an intervening segment to bring testes of x into association with male funnels formerly in xii, gave *Drawida*.

Various sorts of evidence, including some from *Syngenodrilus*, were cited in support of the contraction theory. 1) The epithelium lining the moniligastrid testis sacs requires the cavity of the sac to be coelomic. 2) Trabeculae, within the sac, were thought to be remnants of former septa. 3) The ovarian chamber of various moniligastrids has only to be separated into discrete halves along with loss of nephridia to reproduce identically the testis sac condition. 4) Similar contractions are said to be under way in various megadrile families.

Although Michaelsen's criticisms now appear unimportant, contraction still is unacceptable and for the following reasons. 1) Expansion of *Syngenodrilus* testis sacs involved misinterpretation of figures and text of an inadequate and, in part, erroneous characterization of the type species. Independent examinations of the type (Gates 1945, and Pickford, 1945) found testis sacs to be membranous enclosures of small portions of coelomic cavities. These sacs are in no way comparable to the so-called testis sacs of moniligastrids and there had been no reduction in size of testis segments. 2) Desmogaster gonads

were assumed to be one segment in front of the locations mentioned in the literature. Subsequent investigations have confirmed the original records. 3) Evolution of the moniligastrid ovarian chamber has involved no reduction in size of the ovarian metamere. Essentially, all that has happened is a partitioning off from the rest of the coelomic cavity of a portion containing the ovaries, nephridia and oviduct funnels. Halving the sac and eliminating nephridia would leave size of ovarian segment unchanged and would not provide sacs homologous with those containing the testes. 4) Similarly, supposed contractions in *Acanthodrilus, Hoplochaetella* and *Eutyphoeus,* as well as various changes in other genera, all involve subdivision of coelomic cavities but always without any real decrease in volume of coelomic space or in size of metameres. 5) Moniligastrid testis sacs (cf. p. 301) have no real cavity and no internal epithelium aside from the male funnel. Trabeculae are only muscle strands without peritoneal covering.

The moniligastrid problem was made unnecessarily difficult by the phylogenetically-based classical system in which *Drawida* is directly descended from *Desmogaster.* If *Eohippus* could not remain *Eohippus* during all of the time it was evolving into *Equus, Desmogaster* is unlikely to have remained *Desmogaster* while evolving into *Drawida.* Hence *Drawida* ovaries of xi and *Desmogaster* testes of xii, as well as other aspects of the puzzle, can be considered separately and independently rather than simultaneously.

The *Drawida* condition can be derived theoretically from the ancestral octogonadal battery by elimination of the ovaries in xiii and the testes of x along with excalation of one segment in front of the gonad region. The gonads thus eliminated did disappear in evolution of the Enchytraeidae — if that family has a common ancestry with megadriles. The required excalation has been made (cf. below) in another family.

The *Desmogaster* condition cannot be derived by any of the evolutionary changes recognized in the classical system. Here also the problem was made unnecessarily difficult by an assumption of gonad immutability. Although never so stated, construction of the basic phylogeny proceeded as if the sexual nature of each gonad in the ancestral battery already had been irreversibly determined. Studies of parthenogenetic morphs by the author have shown that any testis can become hermaphroditic or even an ovary of different and distinctive shape. Determination of

gonads for maleness accordingly is reversible. Although that discovery is of no help in solving the *Desmogaster* problem, it does provide a second method of deriving the *Drawida* condition from the octogonadal battery, *viz.*, by elimination of gonads in xii and xiii along with conversion of testes in xi to ovaries. Conversion of ovaries to testes has not been found in the author's morphs and is not to be expected in series hitherto studied, as oligochaetes seem to have an innate prohibition against evolution of dioecism.[4] The literature does, however, contain various records of gonads in xii of normally metagynous species — those in which the gonads of xii usually abort ontogenetically. Unaborted gonads of xii in such individuals were ovaries, hermaphroditic, or even testes. The *Desmogaster* condition then can be derived merely by eliminating from the ancestral octogonadal battery the testes in x and by conversion of ovaries in xii to testes.

Gonadal batteries of two megascolecid genera, *Tonoscolex* and *Nelloscolex* Gates 1933 and 1939, with testes in ix-x and ovaries in xii, obviously can be derived only by excalation of one metamere in front of the gonad region. Fortunately, somatic as well as reproductive organs from the gizzard and posteriorly are one segment anterior to normal location. The excalated segment must then have been one of the first four or five. Just how the excision could have taken place is shown by changes now under way or recently made in various megadriles. The intersegmental furrow demarcating the first from the second segment, even when preservation is optimal, often is indistinct. That same furrow, along with the prostomium, has disappeared in *Pontoscolex corethrurus* (Müller, 1856) and the first two segments have become so small that together they are markedly shorter than the third. Actually, only presence of setae just in front of the first intersegmental furrow (originally 2/3) enables recognition of the fusion, just as in the apparent peristomium of the leech-like oligochaete (cf. above p. 298), *Acanthobdella peledina* Grube, 1851, and in *Trichodrilus cantabrigiensis* (Beddard, 1908). Elimination of the setal follicles originally belonging in ii, that is now under way in various species, when completed will produce the elision required by *Tonoscolex* and *Nelloscolex*.

Also noteworthy in the same connection is the derogation of metameric organization anteriorly that has become common, presumably subsequent to retraction of the brain into the region of

[4] All supposed cases of dioecism now have been found to be instances of genital polymorphism in which the morphs have evolved after establishment of parthenogenesis.

segment iii and of the united cord ganglia of i-iii to a slightly more posterior level. Among those long known "cephalizations" are various abortions, presumably often ontogenetic: of setal follicles in ii as well, sometimes, as several successive segments; of portions or all of one or more of septa 1/2-4/5; of nephridia in ii or occasionally even in additional segments as far back as x-xiv; of parts or all of vascular commissures between dorsal and ventral trunks in ii-iv or v, of the dorsal trunk itself and back to hearts of vi, vii, viii or even ix.

Excalation of one segment, along with elimination from the octogonadal battery of one pair of ovaries and/or one pair of testes provides gonadal conditions in most microdriles. Two exceptional lumbriculid genera, *Styloscolex* and *Premnodrilus*, require two segments to have been elided. Even for that derivation evidence is provided by location of somatic as well as genital organs in an unnamed glossoscolecid (Gates, MS) at least two, possibly three, segments in front of the usual positions.

Gonadal conditions in the few remaining microdriles, Aeolosomatidae and Naididae, can be derived theoretically from the ancestral battery by elisions of 4, 6 or 7 segments. For so much excalation no evidence has been found. A different way of bringing naids into a common line of oligochaete descent requires further consideration of the genital conservatism that is basic in the classical system.

The only changes allowed in the gonadal series during the entire period of megadrile evolution are elimination of a pair of testes and/or of one pair of ovaries. The author's studies of parthenogenesis have shown that all reproductive organs, except the clitellum, ovaries and female gonoducts, can disappear in such a short time as to allow no evolutionary changes in specifically distinctive, somatic structure. Although genital evolution presumably is slower in sexually reproducing forms, opportunity for many more than the one or two gonad eliminations of the classical system does seem to have been provided during the Tertiary and Quaternary. Former existence of a longer ancestral series, with gonads at least in segments v-xviii, now is suggested because of the following facts: 1) Location of ovaries in two species of *Haplotaxis* as far back as xv-xvi, gonads formerly in xii-xiv presumably eliminated. 2) Occasional presence in lumbricid individuals of ovaries in some or all of xiv-xviii. 3) Occasional presence of ovaries in xiv of individuals belonging to four other families. 4) Presence of gonad anlage in xii of embryos, various species (3 families) with

no gonads in that segment of adults. 5) Presence of testes in ix of occasional ocnerodrilid and microchaetid individuals. 6) Presence of testes in some or all of segments v-ix, all individuals of one common, parthenogenetic morph of *Pheretima anomala* Michaelsen, 1907 (cf. Gates, 1956), of especial interest in connection with the Naididae where testes are in one of segments iv-vii. 7) Gonads in as many as nine segments of head regenerates, several species of *Perionyx*. 8) Gonads in as many as twelve segments of some head regenerates of *Criodrilus lacuum* Hoffmeister 1845.

An ancestral battery of more than eight gonads was suggested by Yamaguchi (1953), but it was characterized only as polytesticulate and without specification as to axial extent.

Presence of supernumerary gonads in unregenerate individuals (one exception, below) is regarded not as a novelty but rather as a reversion to an ancestral condition. That viewpoint seems to be required by the fact that in all sexual megadrile populations reduction rather than extension of gonad series is involved. Indeed, one pair of testes has been lost so recently that the associated but now functionless gonoduct funnels still are present in adults of various species belonging to several families.

Supernumerary gonads in segments produced by halving of mesoblastic somites during early embryonic development (Gates, 1960a) are not cited in support of a longer gonadal series in the megadrile ancestry. Nor was abortion of embryonic somites cited as a method of segment elision. Causation of both anomalies now seems likely to be extrinsic. If, on the contrary, causation can be intrinsic, mechanisms for evolutionary provision of Beddard's intercalations and excalations could be available.

Testes must have been anterior and ovaries must have been posterior in the polygonadal battery now proposed, as such sequence is universal throughout the Oligochaeta. Polygonadal homomorphic head regenerates (*Criodrilus* and *Perionyx* spp.) also have the same order. Even in heteromorphic head regenerates sequence is reversed only with respect to the major axis of the substrate. Anteroposterior axiation of the gonadal battery in the male-female order seems to have been rigidly determined early in oligochaete evolution. Some of the data cited above hint that the first seven pairs of gonads might have been male but in polygonadal batteries of regenerates a variable number of pairs towards the middle of the series often is hermaphroditic. Further specification as to the ancestral battery seems unnecessary because of the mutability of gonad sex already proposed above.

Oligochaete gonads develop on septa from which they usually proliferate posteriorly. The peritoneal covering eventually ruptures releasing gonocytes into the coelomic cavity of the gonad segment or into some partitioned off portion of that cavity. Passage thence to the exterior is by way of ducts opening into cavity of the gonad metamere through a funnel located on the anterior face of a septum and opposite the gonad. Proliferation in the funnel anlage at first is anteriorly and toward the developing gonads but soon is reversed with the result that the ducts grow away from both organs. Moniligastrid testes, the exception to the general rule, proliferate into the interior of their septa. This unique reversal of direction in gonad proliferation, presumably established early in evolution of the family, always is associated with an intraseptal location of the male funnels. Moniligastrid phylogeny, according to the classical system, required an interseptal transfer of male funnels, in case of *Drawida* from the anterior face of 10/11 or a more posterior septum into interior of 9/10. The gonad-funnel association, whether of the moniligastrid sort or otherwise, is so constant even in aberrant individuals as to suggest some sort of causal relationship. If development of either organ is induced by the other the stimulus is more likely to emanate from the gonads and especially since they seem to be the first to appear. Control, then, is effected in the direction of proliferation. Moniligastrid testes though growing into the septum rather than away from it still exert their influence on the nearest susceptible tissue. As a result early proliferation of funnel anlage also is into, instead of away from, the septum but still toward the testis which may even be surrounded at maturity.

Absence of one member of the gonad-funnel association, in the cases hitherto observed, provides no special difficulties. 1) Gonads at testis sites in x and/or xi, funnels lacking. This condition is found in certain male sterile parthenogenetic morphs of various species. Inductive capacity apparently has been lost along with fertility. 2) Ovaries, at testis sites in x and/or xi, funnels lacking. A condition also found in parthenogenetic morphs. These gonads appear to develop more slowly than the ovaries at the usual site in the same animal. Susceptibility to funnel induction may be lost before the inductive influence became effective. 3) Male gonoduct funnels present in x, testes lacking. The anterior funnels often are present in sexually reproducing metandric species and may be continued into more or less normal ducts. The testes, in such cases, abort but only after funnel

development had been induced. Considerable variation in completion of funnel development after initial induction may be associated with differences in time at which the gonad begins to regress.

The octogonadal battery in which gonad nature was irreversibly determined made derivation of microdriles and megadriles from a common ancestor difficult. A polygonadal battery of the sort suggested above permits that derivation economically and by processes now under way or recently completed in extant forms. Gonoduct funnel induction by the gonads, with similar economy, gets moniligastrid funnels into their septa.

Speculation about oligochaete phylogeny, in absence of valid fossil records and in accordance with previously stated assumptions (Gates, 1960b, p. 281), involves estimating comparative stability of organization during long periods of evolution. If structure rather generally shared by extant oligochaetes has not changed uniformly since the Jurassic or Cretaceous[5] a distant ancestral type may have been characterized somewhat as follows. Body, with homonomous metamerism internally as well as externally. Prostomium, without appendages and simple in comparison with the polychaetes. Setae, no longer in parapodia, in longitudinal ranks of four bundles per segment. Musculature in two layers, the longitudinal internal to the circular of the body wall. Septa, present between all segments. Digestive system, with short buccal cavity, glandular pharynx, simple esophagus and intestine (without special gland diverticula and typhlosoles). Vascular system, with dorsal and ventral trunks connected directly or indirectly in each segment by a pair of commissures. Excretory system, with segmentally paired, simple nephridia each with a preseptal funnel and a postseptal body opening directly to the exterior by a duct in its own segment (presumably ventrally if not close to *B*?). Nervous system, with a simple cerebral ganglion, circumpharyngeal connectives to a subpharyngeal ganglion, a single ventral nerve cord of double origin with a ganglionic widening in each segment, possibly also three pairs of nerves per segment. Hermaphroditic. Gonads, on posterior faces of septa near ventral parietes and nerve cord, as suggested above one pair in each of a number of segments (perhaps 12 or 13), in a continuous series with testes anteriorly.

[5] *Cf.* Stephenson, 1930, p. 706. The author has no brief for any of the estimates that have been advanced as to age of the oligochaetes.

Oviducts of most oligochaetes are short, straight, opening directly to the exterior in the segment next behind that containing their funnels. Divergence often is associated with some special condition, e.g., dislocation of septal insertions on the parietes, that obviously is of recent origin. A primitive structure accordingly appears to have been retained rather generally. Male gonoducts of some microdriles are of the same simple kind. Elongated ducts in other oligochaetes usually are associated with special conditions unlikely to have characterized a common ancestral form. Accordingly, all gonoducts of the oligochaete precursor are assumed to have been of the same sort regardless of the gametes they evacuated. All reproductive apertures were minute, superficial, as female pores still are today, and presetal in a middle portion of the ventrum.

Glands of a simple sort, invaginated from the epidermis, are assumed to have been present in the gonad-containing portion of the body. Originally they may have opened into or close beside setal follicles. Some of those "X" glands evolved into various sorts of atria and prostates many of which still develop near setal follicles of the ventrum. Other X glands, judging from the similarity of prostates and spermathecae in certain primitive ocnerodriles, became modified for storage of foreign sperm. In such cases, association with follicles was exchanged for invagination at intersegmental levels.

With appearance of a clitellum (possibly unilayered at first), worms would have been recognizable as oligochaetes. Cocoons now could be secreted for protection of developing young. Sperm could be stored for repeated fertilizations. Profuse production of gametes, in a polychaete manner, no longer was necessary. Henceforth, one of the more important aspects of oligochaete evolution was to be reduction of gamete production and eventually development of more effective means of economic exchange of sperm. The earlier change may not have come about by an immediate elimination of testes and ovaries but rather by establishment of differential rates of maturation throughout the gonad battery. This, at first, may have allowed breeding by each individual to continue through longer periods. As differences in rate of development became more marked some gonads still would be juvenile at death or when breeding was terminated by interposition of unfavorable environmental conditions such as drought. Juvenile gonads would have been associated, just as in various forms today, with functional gonoducts. As a result

of further accentuation of developmental rates, death or termination of breeding would come before funnel and gonoduct development had been induced. Gonads, however, still would have been recognizable as such in early embryonic stages just as those of the twelfth embryonic somite still are in various metagynous earthworms. Eventually, primordial germ cells perhaps would not be aggregated into structures recognizable as definitive gonads even in embryos. Nevertheless, ability to form gonads in sterile segments long was retained. This is demonstrated by occasional presence of juvenile gonads in segments xiv-xviii of certain adult lumbricids as well as by the juvenile testes in v-ix of adults belonging to one parthenogenetic morph of *Pheretima anomala,* a species of a highly specialized and fairly recently evolved genus. In the latter case, the extra testes may be associated with male funnels and even with more or less perfectly developed male gonoducts. Sterilization in the polygonadal battery doubtless proceeded variously. Early in oligochaete evolution, for instance, posterior gonads may have become sterile in lines leading to certain microdrile families while anterior gonads were aborting in a line leading to the Haplotaxidae. Or, in a line or lines leading to other megadriles the change may have affected both ends of the ancestral battery more or less simultaneously.

The number of setae in a bundle also was reduced. Simplification of setal form got under way, finally ending in the sigmoid sort. Before those changes were made, stocks that were to give rise to naid and tubificid families separated off from the main line of evolution. Other stocks that were to become enchytraeid and lumbriculid presumably split off only after trends to simple shape and lumbricin number had gotten well under way. In a line leading to modern megadriles, the four bundles became four pairs of follicles in each of which development is staggered so that only one seta at a time is functional.

An early megadrile probably should be credited with an esophageal gizzard, perhaps in segment v, and two pairs of simple monaxial spermathecae opening by minute and superficial pores in the ventrum at 7/8-8/9.

Any consideration of subsequent evolutionary changes that led to differentiation of most megadrile families must be postponed until much more information becomes available about anatomy and histology of structure that was derogated in the classical phylogenies.

As just hinted, slowly accumulating evidence provides no reason for believing that families and subfamilies can be filiated in straight line sequences in the classical manner. Similarly, the generic filiations of the mother-daughter-granddaughter sort that constituted the more or less esoteric basis of the classical system appear to be improbable when not already known to be impossible. Various classical assumptions such as those of gonad conservatism and irreversibility of sex determination now have been considered and are found to have prevented understanding of evolutionary developments. Restriction of evolutionary importance to a very few pairs of simple characters did of course enable phylogenies of the *Eohippus* to *Equus* sort, but prevented accumulation of data, especially with reference to the circulatory systems, that could have permitted further consideration of megadrile evolution. Variation in gonad location along the anteroposterior axis of extant oligochaetes now can be explained in one or more of several ways, including elimination of gonads at one or the other or both ends of a polygonadal ancestral battery, by change of sex of either sort of gonad though always with retention of the anteroposterior male-female order, by elision of one or two segments at the anterior end of the body in the course of a cephalization process that is common. The classical descriptive terms, holandry and hologyny are inapplicable in certain situations but remain useful only with reference to conditions recently derived from an octogonadal battery with testes in x-xi and ovaries in xi-xii.

REFERENCES

Avel, M.

1959. Classe des Annélides Oligochètes. *In:* Grassé, P. P. (ed.), Traité de Zoologie, **5**(1): 224-470.

Beddard, F. E.

1891. Observations upon the structure of a genus of Oligochaeta belonging to the limicoline section. Trans. Roy. Soc. Edinburgh, **36**: 5-7.

1895. A monograph of the order of Oligochaeta. Oxford, xxi + 769 pp.

Gates, G. E.

1925a. Some new earthworms from Rangoon, Burma. Ann. Mag. Nat. Hist., (9) **15**: 317-328.

1925b. Some new earthworms from Rangoon, Burma. II. *Idem*, (9) **16**: 49-64.

1925c. Note on a new species of *Drawida* from Rangoon, Burma. *Idem*, (9) **16**: 660-664.

1929. A summary of the earthworm fauna of Burma with descriptions of fourteen new species. Proc. U. S. Natl. Mus., **75** (10): 1-41.

1945. On the oligochaete genus *Syngenodrilus* and its taxonomic relationships. Jour. Washington Acad. Sci., **35**: 393-396.

1956. Reproductive organ polymorphism in earthworms of the oriental megascolecine genus *Pheretima* Kinberg 1867. Evolution, **10**: 213-227.

1959. On a taxonomic puzzle and the classification of the earthworms. Bull. Mus. Comp. Zool., Harvard College, **121**: 229-261.

1960a. On another biclitellate earthworm. American Midland Nat., **63**: 418-423.

1960b. On Burmese earthworms of the family Megascolecidae. Bull. Mus. Comp. Zool., Harvard College, **123**: 203-282.

MICHAELSEN, W.

1900. Oligochaeta. Das Terreich, vol. 10, xxix + 575 pp.

1921. Zur Stammesgeschichte und Systematik der Oligochäten. Arch. Naturgesch., **86** (A-8): 130-141.

1922. Die Verbreitung der Oligochäten im Lichte der Wegener'schen Theorie der Kontinentverschiebung. Verhandl. Ver. Naturwiss. Hamburg, (3) **29**: 45-79.

1928-1930. Oligochaeta. *In:* Kükenthal and Krumbach, Handbuch der Zool., **2** (2-8): 1-118.

PICKFORD, G. E.

1937. A monograph of the acanthodriline earthworms of South Africa. Cambridge, England, 612 pp.

1945. Additional observations on the oligochaete genus *Syngenodrilus*. Jour. Washington Acad. Sci., **35**: 397-399.

1948. Article, Annelida, Class 2. Oligochaeta. Encyclopedia Britannica, 14th ed., vol. 1, pp. 998-1006.

STEPHENSON, J.

1922. Contributions to the morphology, classification and zoogeography of Indian Oligochaeta. V-VI. Proc. Zool. Soc. London, 1922:119-148.

1923. Oligochaeta. *In:* Fauna of British India including Ceylon and Burma. London, xxiv + 518 pp.

1930. The Oligochaeta. Oxford, xiii + 978 pp.

YAMAGUCHI, H.

1953. Studies on the aquatic Oligochaeta of Japan. VI. Jour. Fac. Sci. Hokkaido Univ., (6. Zool.) **11**: 277-342.

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A STUDY OF *ECHMATEMYS CALLOPYGE* FROM THE UINTA EOCENE OF UTAH, AND ITS REDEFINITION AS A SUBSPECIES OF *E. SEPTARIA*

BY DAVID C. ROBERTS

WITH TWO PLATES

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No. 6 — A Study of *Echmatemys Callopygc* from the Uinta Eocene of Utah, and Its Redefinition as a Subspecies of *E. Septaria*

By David C. Roberts

INTRODUCTION

On September 2, 1953, my field partner Dee A. Hall and I independently located a shell of *Echmatemys* in Uinta Lower C mudstone of Devil's Playground, north of Bonanza, Uintah Co., Utah. We were at the time collecting for the Utah Field House of Natural History in Vernal. The removal of the shell resulted in the discovery of a turtle quarry, which we worked twice during the next summer, uncovering no less than 43 shells and collecting 14. All but one of the latter I identified as *Echmatemys callopygc* Hay; the exception was *E. uintensis*. The second time we worked the quarry in 1954, we noticed that it had become the "mother lode" of the Wampus Cat No. 2 uranium claim in our absence, a fine tribute to the radioactivity of the bone.

During these and other trips to the locality, we also collected five turtles in the near vicinity of the quarry; one was *E. uintensis*, and the others were *E. callopygc*. Subsequently, for the Cleveland Museum of Natural History, I revisited the Wampus Cat No. 2 in 1956 and 1958, and with various assistants removed ten reasonably complete shells and an isolated plastron. Six of the quarry specimens are as yet unprepared, but field identifications indicate that they pertain to *E. callopygc*. The other four are definitely this species. The quarry and its surroundings, then, have yielded 23 to 29 specimens of *Echmatemys callopygc*.

Gilmore (1945) has described a similar *Echmatemys* quarry in Wyoming. The matrix has formed apparently from a pond deposit consisting of reworked volcanic ash and ordinary clay. Although the skeletons were not articulated, the shells were all found right side up.

In the Wampus Cat quarry, the shells were found lying in all possible positions. The matrix undoubtedly was laid down as silt on the bottom of a pond or lake. It may be imagined that the turtles congregated about or within the diminishing margins of a pond that was drying up, and eventually starved. Later, the pond presumably filled up again, and mud flow action on its bottom rolled the shells around and distributed the limb

and girdle elements throughout the matrix. Both quarries share the same frustrating lack of skulls and vertebrae.

Mr. Thomas H. Hawisher, a geologist with the Ferro Corporation of Cleveland, has very kindly examined a sample of the Wampus Cat quarry matrix, and his report is as follows (personal communication):

"The rock is best classified as either a highly calcareous mudstone or marlstone. Irregular lumps of clay, fossil fragments, and small, thin sheets of calcite are dispersed in a matrix of argillaceous material and microcrystalline calcite. The matrix itself is mottled as a result of irregular cementation by the microcrystalline calcite.

"The rock is composed almost entirely of two constituents: argillaceous material and calcite. These represent approximately 45 and 50% respectively. The balance consists of quartz, cristobalite, and possibly a number of trace minerals.

"The mineralogical composition of the argillaceous material defies accurate determination by microscopic, x-ray, and differential thermal analysis methods. It is apparently a rather complex mixture of several clay minerals which are perhaps partly amorphous.

"Calcite occurs as three distinct types; microcrystalline ooze mixed with argillaceous material, aggregates of fine crystals, and thin sheets or crusts less than one millimeter thick and oriented variously. These crusts consist of fine calcite crystals whose orientation is not related to bedding planes, thus suggesting precipitation along cracks rather than fossil replacement or lamellar deposition on a bedding surface.

"Quartz is present as angular grains of very fine sand and silt size disseminated throughout the matrix. Cristobalite was not positively identified microscopically but was detected by x-ray diffraction techniques.

"Although it is difficult to speculate on the environment of deposition without a field study, the petrography of the rock suggests some possibilities. The relative proportion of clay and calcite and the lack of coarse grained material suggests slow accumulation in relatively quiet water. This, coupled with the fact that the Uinta Formation is a terrestrial deposit, indicates that the environment was a fresh water lake. Perhaps it was a lake developed on the flood plain of a large river, but it is impossible to be certain without detailed mapping.

"The presence of cristobalite raises the possibility that (like at the Wyoming quarry) there may have been volcanic activity

at the time of deposition. However, with the exception of the cristobalite, evidence of volcanism such as glass shards, crystal fragments, etc. is lacking. It is perhaps best to assume that the cristobalite represents material brought in with the quartz and argillaceous material as detritus from an older source area or as wind blown sediment from a far distant area of volcanic activity."

The only fossil remains observed at the Wampus Cat quarry which were not of a chelonian nature were two small crocodilian teeth and a fragmentary crocodilian scute.

Aside from Devil's Playground, some energetic and dedicated associates and I collected a large number of specimens of *Echmatemys callopyge* at several localities between 1952 and 1959. These are presently in the collections of the Utah Field House, the Museum of Comparative Zoology, and the Cleveland Museum of Natural History. The quarry specimens are housed at the three above-mentioned institutions plus the American Museum of Natural History and Upsala College. Counting the type at the American Museum, a specimen at the United States National Museum, and four at the Carnegie Museum, the total number of individuals which I have examined is an amazing 54. There are also two series of limb and girdle elements from the matrix of the quarry. As might be expected, many of the shells are more or less incomplete, but all have contributed to this study. All specimens are from B and C members of the formation. Due to crushing and distortion in many of the specimens, the measurements used are not necessarily exact, but I believe they are close enough to render the conclusions derived therefrom undeniable.

The similarity between Hay's species and *Echmatemys septaria* from the Bridger Eocene of Wyoming suggested a close comparison between the two long-standing forms. The results of my investigation strongly indicate that the two are actually conspecific, but that the Uinta turtle is a subspecies of the Bridger one.

COMPARISON OF *E. CALLOPYGE* AND *E. SEPTARIA*

Hay (1908) described *Echmatemys callopyge* from a single shell in the American Museum of Natural History, No. 2087. He characterized it primarily on the proportions of the first vertebral scute and the formation of the plastron's anterior lobe (p. 341).

"The anterior lobe is slightly contracted just in front of the axillary notch; then expands a little to the ends of the epiplastra; then curves slowly to the truncated lip. The latter is unusually narrow . . . being less than one-fourth of the width of the anterior lobe. It is markt outwardly on each side by a stout tooth, mesiad of which there is a notch . . . On the upper side of the bone there is, along the midline, a prominent ridge . . . bounded on each side by a valley . . ."

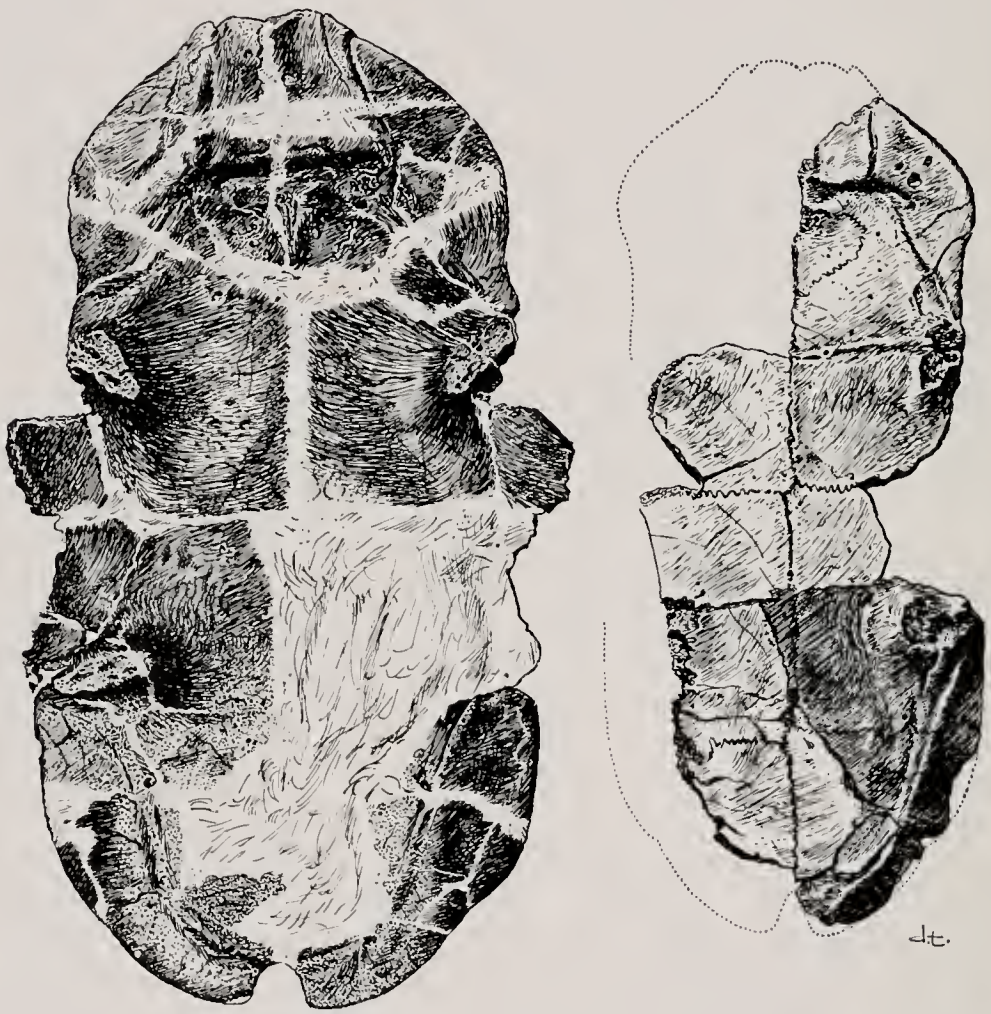

Fig. 1. *Echmatemys septaria*. Internal view of plastron. Left, *E. s. callopyge*, typical specimen (MCZ 2976); right, *E. s. septaria*, type (USNM 4088) (x ¼).

The first vertebral scute is described by Hay as "unusually narrow"; its length is 139 per cent of its width in the convex central portion. The lateral margins of scutes 2, 3, and 4 are "bracket shaped," and although the scutes are "longer than

broad,'' they are ''rather broad.'' The last observation is certainly true when comparison is made with some other species of the genus.

In Hay's opinion, on the basis of the only specimen available, the relative narrowness of the first vertebral scute justified the separation of his new species from all other known members of the genus, while other useful characters were the broad central vertebrals, the narrow epiplastral lip, and the ''longitudinal ridge on the upper side of the symphysis'' of the epiplastrals.

Among the first results of my examination of specimens from the Wampus Cat quarry was the realization that the relative width of the first vertebral scute is quite variable, and therefore is of little value for a specific determination. This conclusion was long ago suggested by Gilmore (1915, p. 125), but since he had only two specimens, he did not change the nomenclature. Collecting in other localities than Devil's Playground has added to the total number of carapaces with the first vertebral preserved, and has proven Gilmore's contention. In 22

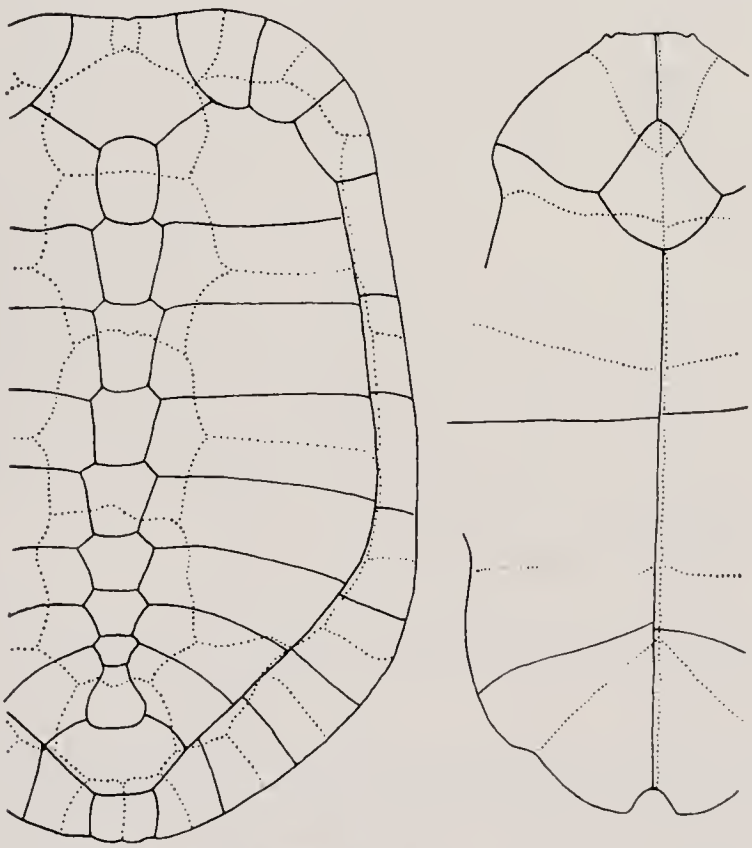

Fig. 2. *Echmatemys septaria callopyge.* Diagram of plastron and carapace of a typical specimen, with relatively wide first vertebral scute. Drawn from MCZ 3125.

adults, not including those mentioned by Gilmore, the length/width ratio varies from 1.39 in the type to 0.81. The mean is 1.10 (Figure 2; Plate 2). In these cases, the width is across the central or posterior convexity, depending upon the shape of the scute.

The other specific attributes mentioned by Hay — the broad central vertebrals, the narrow epiplastral lip, and the median upper ridge on the lip — can all be found in Bridger *E. septaria*. It would appear, then, that there is little basis for the retention of *Echmatemys callopyge* as a distinct species, in the light of information gained from a larger series of shells. All of which again proves Gilmore's oracular prowess. In his Uinta turtle paper (1915, pp. 126, 127), he wrote:

"Had *E. callopyge* not been established, I should have unhesitatingly referred both of the specimens discussed above to *Echmatemys septaria* (Cope). For the present, however, it will serve all purposes to assign them to the established Uinta species . . ."

Hay's description of *E. septaria* is closely comparable to that of his Uinta species, if the first vertebral scute be excepted. What he wrote about the anterior plastral lobe of AMNH No. 6085[1] mirrors the above quoted statements about that area in the *callopyge* type. Hay (1908, pp. 321-322) stated:

"Immediately in front of the axillary notch the lobe narrows a few millimeters, then begins to expand and becomes wider than at the base. At the hyoepiplastral suture the lobe narrows again and passes rapidly to the lip. This is relatively narrow . . . is notcht at the midline, and is furnisht on each side with a blunt tooth. The epiplastrals thicken toward the lip and become 20 mm. thick. For some distance on each side of the symphysis of the bones the thickness is redueed to 15 mm. The lateral expansion of the anterior lobe and the lip form the most distinctive characters of this species."

Hay classified the second and third vertebral scutes as "urn-shaped, expanded in front and narrowed behind." Such a shape, particularly in the second scute, is characteristic of the Uinta turtles as well.

Through the kindness of the Utah Field House, the Carnegie Museum, the American Museum, and the United States National Museum, I have been able to study eleven individuals which,

1 Abbreviations for institutions used in this paper are as follows: AMNH, American Museum of Natural History, New York; CM, Carnegie Museum, Pittsburgh; CLM, Cleveland Museum of Natural History; UFH, Utah Field House of Natural History, Vernal; USNM, United States National Museum, Washington.

in my opinion, all belong to the species *septaria*, and which are from the Bridger Formation. Among these are the type, two of the American Museum specimens studied by Hay, and five from the Levett Creek Quarry in Wyoming reported on by Gilmore (1945). I disagree with Gilmore's identification of the Levett Creek specimens as *Echmatemys wyomingensis* primarily because they show a greater longitudinal development of the epiplastral lip than would appear to be the case in *E. wyomingensis*. Admittedly, the lateral expansion of the anterior lobe in the quarry shells observed is poorly developed when compared with the *septaria* type, but this character is variable in the Utah individuals, so presumably the same holds true for those from Wyoming as well. The shells from the same locality in the Carnegie Museum were identified as *E. septaria*. I am also including an exceptionally fine specimen from the United States National Museum collection (No. 16687) which was labeled *E. aegle*, but which I do not believe can be separated from *septaria* (Plate 1). Such is probably the case with several of the published Bridger species of *Echmatemys*, although a greater knowledge of the Bridger turtle fauna will be necessary to prove or disprove it.

When a comparison was made between the Bridger and Uinta turtles which I studied, in 15 different characteristics, the results fell into three general categories:

1. Little or no difference
   Width anterior lobe at base/length anterior lobe on the mid-line
   Width posterior lobe at base/greatest length posterior lobe
   Distance between epiplastral teeth/width anterior lobe at base
   Width anterior lobe at base/overall length plastron
   Second neural—length on mid-line/greatest width
   Fourth neural—length on mid-line/greatest width
   Third vertebral—length on mid-line/width in middle
   Encroachment of axillary and inguinal buttresses on the plastron
2. Means different, but ranges of variation overlapping
   Length epiplastral lip on upper side/length hyoplastron where it reaches the mid-line
   Length entoplastron on mid-line/greatest width entoplastron
   Length nuchal bone on mid-line/greatest width nuchal bone
   First vertebral—length on mid-line/width in middle
   Second vertebral—length on mid-line/width in middle
3. Means different, ranges of variation barely meeting
   Length epiplastral lip on upper side/length anterior lobe
   Length epiplastral lip on upper side/overall length plastron

The ratios are summarized in Table I.

There is a discernible difference in the plastron length (and other dimensions) of presumed fully mature individuals, with the Uinta form the larger. It seems illogical to consider that all of the six complete *septaria* specimens were smaller than average mature adults, although it is possible, and the small number of plastra measured renders the statistics somewhat questionable. However, the other five specimens, whose plastra were not complete, were similar in size.

The difference which I consider most significant is in the degree of development of the epiplastral lip on the upper surface. This is a characteristic which has been relatively neglected in *Echmatemys,* as in other Eocene turtles, due to the fact that many of the specimens have not had the matrix removed from the insides of the shells. In the turtles of the Uinta Formation, the development of the lip plus the general contour of lip and lobe make identification of the species comparatively easy, even in the field.

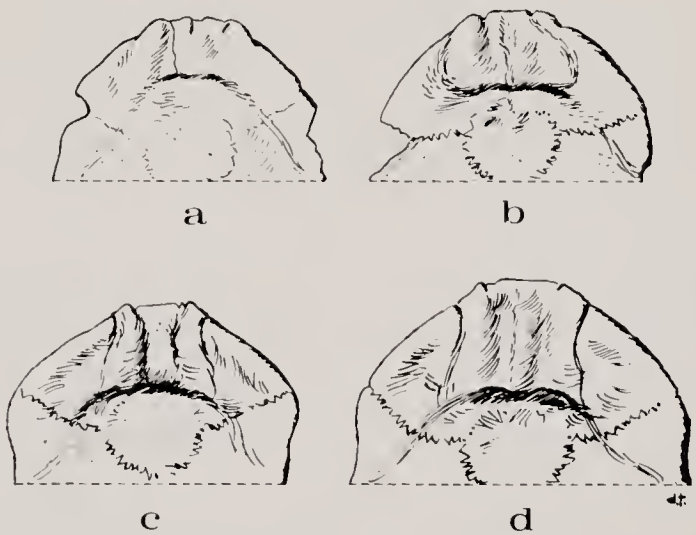

Fig. 3. Epiplastral lip development in *Echmatemys septaria. a,* minimal development, *E. s. septaria* (CM 11923); *b,* medium development, *E. s. septaria* (UFH 228-2); *c,* medium development, *E. s. callopyge* (MCZ 3124; *d,* maximal development, *E. s. callopyge* (MCZ 3125) (x ⅕).

When the mid-line length of the thickened lip is related to that of the anterior lobe, or the length of that portion of the hyoplastron which reaches the mid-line, or the overall length of the plastron, it is seen to be relatively greater in the Uinta turtles than in those of the Bridger. This gives a well developed

callopyge anterior lobe a much more massive appearance than even an above average *septaria*. If a maximal callopyge be compared with a minimal *septaria* in this respect, one might hesitate to call the two the same species, but if a series is laid out, the variants visually as well as statistically grade one into the other (Figure 3). No doubt it is possible that were more specimens available, the ranges of variation in this characteristic would be found to overlap. I believe that the few significant differences between the Wyoming and Utah turtles are best explained as more extreme developments in the latter of characters already found in the former, i.e., the epiplastral lip length and size. Bridger individuals could have migrated into the Uinta Basin through the contemporary (and lower) Uinta Mountains and there could have formed a relatively isolated population, so that by Uinta B times a slightly different shell could have evolved.

All the evidence implies that there is no solid basis for a specific distinction between the Uinta and Bridger forms, although they are not exactly the same. I therefore propose that the Uinta turtle be considered as a subspecies of the earlier described *Echmatemys septaria*.

FORMAL DESCRIPTION

Echmatemys septaria (Cope)

Eocene pond turtles with moderately high carapaces, and plastra up to about 45 cm. in overall length. Anterior lobe of plastron about 1½ times as wide at its base as its mid-line length; width at base somewhat less than half the overall length of the plastron. Anterior lobe usually with a distinct marginal concavity between the base and the hyoepiplastral suture, giving the edge of the lobe a more or less flattened S-curve. Epiplastral lip narrow, and well developed fore and aft on the upper surface, bearing two obtuse longitudinal ridges on the upper surface just mesiad to the gulohumeral sulci; these ridges ending in bluntly pointed "teeth" of varying distinctness. Longitudinal ridge along mid-line of lip on upper side, with shallow valleys between it and the distal ridges. Distance between centers of "teeth" varying from 20 to 40 per cent of width of anterior lobe at the base. Length of lip on mid-line of upper surface roughly 25 to 50 per cent of anterior lobe length, roughly 35 to 70 per cent of length of hyoplastron where it reaches the mid-line, and about 9 to 14 per cent of overall length of plastron.

Entoplastron pear shaped; about as wide as long, or slightly wider. Entoplastron encroached upon at its anterior end by the gular scutes and crossed by the humeropectoral sulcus somewhere on its posterior half.

Width of posterior lobe of plastron at its base 1¼ to 2 times its length; usually considerably less than twice. Xiphiplastra drawn out into narrowly rounded points, often concave medially and convex laterally, but not always.

Carapace with first neural more or less oval, neurals two to seven hexagonal, with the wide ends pointing forward, neural eight variable. Two suprapygal bones. Vertebral scutes two and three more or less urn-shaped, scute three less so than two. First vertebral scute variable in shape. Free borders of central anterior and posterior peripherals acute, with the anterior ones slightly blunter than the posterior ones.

Echmatemys septaria septaria (Cope)

Emys septaria, Cope, 1873, p. 625
Cope, 1882, p. 992
Cope, 1884, pp. 130, 139
Hay, 1902, p. 448
Echmatemys septaria (Cope), Hay, 1906, p. 28
Hay, 1908, pp. 319-323
Echmatemys wyomingensis, Gilmore, 1945, pp. 102-107
Bridger Eocene of Wyoming. Epiplastral lip on upper side is:
ca. 25-40 per cent of length of anterior lobe
ca. 35-50 per cent of length of hyoplastron where it reaches midline
ca. 9-10 per cent of overall length of plastron
Type: USNM No. 4088

Echmatemys septaria callopyge Hay, New Combination

Echmatemys callopyge, Hay, 1908, pp. 340-342
Gilmore, 1915, pp. 123-127
Echmatemys obscura, Gilmore, 1915, pp. 135-139
Echmatemys hollandi, Gilmore, 1915, pp. 133-135
Uinta Eocene of Utah. Epiplastral lip on upper side is:
ca. 40-50 per cent of length of anterior lobe
ca. 45-70 per cent of length of hyoplastron where it reaches midline
ca. 10-15 per cent of overall length of plastron
Type: AMNH No. 2087

DISCUSSION

In the Uinta Formation, *Echmatemys s. callopyge* can be readily distinguished from the other species of the genus, as has been stated above. My acquaintance with a large number of Uinta *Echmatemys* specimens has convinced me that among the turtles collected up to the time of writing, there are no more than four species involved. These are: *septaria, uintensis, douglassi,* and possibly a fourth, represented by incomplete material, which should be considered either as a new species or as a very unusual variant of *E. septaria.*

E. s. callopyge can be separated from *uintensis* and *douglassi* by its greater development of the epiplastral lip; the observed minimum for the subspecies in question is .10 of the overall plastral length, and in the other species the same ratio is .08 in one specimen of each measured. The detailed form of the epiplastral lip is definitely different from that in *uintensis* and *douglassi,* and the anterior lobe is relatively longer than in the latter. The possession of epiplastral "teeth" distinguishes *callopyge* tentatively from the possible new species. There are other differences as well, which will be fully covered in a future paper on the Uinta turtle fauna.

E. OBSCURA AND E. HOLLANDI

Two of the species erected by Gilmore in his 1915 paper are most likely to be considered as variants of *Echmatemys septaria callopyge.* These are *E. obscura* and *E. hollandi.* I have carefully examined the types (and only specimens) of each, and in each case have restored for the first time the upper side of the anterior plastral lobe — the feature which, among other things, makes their retention as valid species questionable.

The characteristics of *E. obscura* which set it apart from other species were stated to be: the very narrow nuchal bone, the fact that the gular and pectoral scutes reach the entoplastron, the greater relative widths of the neural bones and vertebral scutes, and the obscure longitudinal ridges on the pleural region of the carapace. A comparison of the type with specimens of *E. septaria* shows that the nuchal bone certainly is unusually narrow, but the vertebrals and neurals are characteristic of *E. septaria,* as is the encroachment of the gulars and pectorals upon the entoplastron. The extreme width of the fourth neural bone shown in Gilmore's (1915) drawing on page 137 is due to his misidentification of the suture on the right side. The bone is

only slightly wider than those of provable *callopyge* specimens. Similar ornamentation is observable on the carapaces of a more typical specimen (MCZ 3125) and on CM 3249, the type of *E. hollandi*. MCZ 3131, from the Wampus Cat quarry, shows a beautiful pattern of more obvious ridges both on carapace and plastron.

I have removed the anterior lobe from the matrix, and then conservatively restored the missing portion. It is evident that the lobe and epiplastral lip are characteristically *E. s. callopyge;* the ratio of lip length to length of anterior lobe is close to the mean of other specimens measured.

Thus, the only possible significant difference in the *E. obscura* type is the narrowness of the nuchal bone. However, in view of the anomalies to be found in both Recent and fossil turtle shells, as well as the fact that *obscura* was based upon just a single individual with a nuchal bone longer than wide, but whose every other character can be matched in specimens of *E. s. callopyge*, it seems more appropriate to refer Gilmore's species to the synonymy of *callopyge*.

It seems equally necessary to synonymise *E. hollandi* with *Echmatemys septaria callopyge*. The specific determination was based upon the presence on the first pleural bones of a pair of protuberances shaped like truncated cones, and an associated pair of supernumerary costal scutes flanking the first vertebral. The protuberances are beautifully preserved and obvious, and are, as far as my experience with Uinta turtles goes, unique.

At the time Gilmore's paper was published, there were not many specimens of *Echmatemys* from the Uinta in museum collections, and it was not unreasonable for him to believe that such an amazing specimen might represent a distinct species. However, in five field seasons of varying lengths in the Uinta, neither I nor any of my field partners have seen another such pleural bone. If individuals such as the *hollandi* type were at all common, one would think that at least a few fragments showing the protuberance would have been found. This naturally leads to the conclusion that the type is a very unusual variant of another species.

Considered in this light, the supernumerary costal scutes assume less importance. Analogous extra scutes have been observed in *Bacna* (Gilmore, 1915, pp. 114, 118), and other such scutal peculiarities are readily found in living and fossil forms.

The other characteristics of the *hollandi* type appear to be of the *callopyge* habitus. As Gilmore mentioned, much of the

anterior lobe of the plastron had weathered away, but a mold of the upper surface of most of the missing portion was preserved in the sandstone filling of the shell. I made a cast from the natural mold, cemented it to the original base of the lobe, and then restored the lobe in a generalized manner. It looks very much like another member of the *callopyge* tribe. The ratio of estimated lip length on upper surface to the estimated length of the anterior lobe is about at the minimum of other specimens measured, and thus could probably be equated with them. It is surely within the variation of the species *septaria* as it is herein defined.

Six other ratios which can be obtained from the shell all fall within the variation of *E. s. callopyge*. These are: the width of the anterior lobe/its estimated length; the length/width of neurals 2 and 4; and the length/width of vertebral scutes 1, 2, and 3. The proportions of the entoplastron cannot be determined with any exactitude because of its incompleteness, but it appears to have been pear shaped, as in all but one of the *callopyge* individuals. It can be seen in Gilmore's drawing that the shapes of neurals and vertebrals are like those of *callopyge* specimens.

I can, therefore, see no valid characters for the separation of *E. hollandi* from *E. s. callopyge*.

The Characteristics of E. s. callopyge

The anterior lobe of the plastron is consistently much wider at its base than it is long, the width being from about 1⅓ to 1½ times the length. The lateral indentation in the lobe's margin is also quite consistent, although its development varies (Figure 4). In some cases, it is as distinct as that of the type and the specimens of *E. s. septaria* figured by Hay (1908). In several cases, however, it is poorly defined, and in at least one is virtually indistinguishable. In spite of the usually obvious lateral swelling of the lobe, the width at the base is in most cases the greatest width. In some, the two widths are the same, and in a few, the central width is the greater.

The epiplastral lip varies from decidedly prognathous to extending little if at all from the contour of the lobe (Figure 4), but in all specimens in which it was preserved, its configuration was as defined above. Its thickness ranges from slightly less than a centimeter to almost two centimeters in adults; this is due in many cases to the fact that some are more crushed

than others, but there is evidence that the thickness did vary in life. The epiplastral "teeth" sometimes blend gradually into the margin of the lip, and sometimes are well defined by a mesial groove or emargination; occasionally, there are one or more tiny supernumerary points between the "tooth" and the main body of the lip (as in the type).

The fore-and-aft development of the epiplastral lip is unusually great for an emydine turtle, the minimum length being 10 per cent of the overall plastral length, with a mean of 12 per cent. The same ratio in twelve Recent and fossil emydines ranges from 1 to 10 per cent (Table III). As Hay mentioned, the anterior width of the lip is also unusually small. It appears to be characteristically slightly over ¼ the width of the base of the anterior lobe.

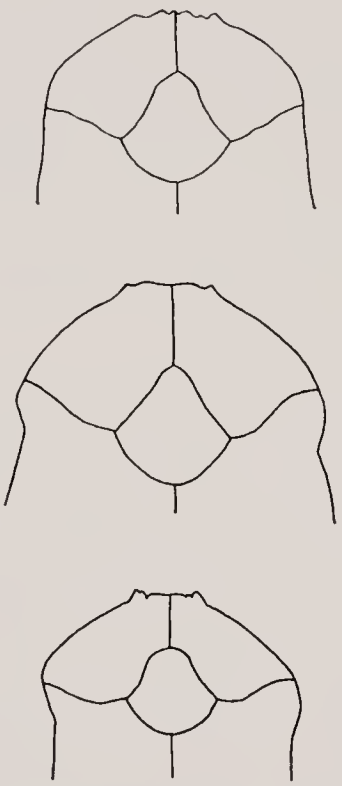

Fig. 4. *Echmatemys septaria callopyge.* Diagrams of three anterior plastral lobes, external view, showing variation in lobe margins and shapes of entoplastra.

The entoplastron is invariably more or less pear shaped, and its greatest length and greatest width are always close. The humeropectoral sulcus crosses it at all levels from its widest section to its posteriormost point, but in the majority of individuals,

the sulcus crosses roughly halfway between those levels. Many, but not all, of the cases in which the sulcus is at or near the posterior point of the entoplastron are immature shells.

The posterior lobe of the plastron in well preserved specimens differs little from that of the type. Its basal width is usually around 1½ times its greatest length, although the range of variation is from less than 1¼ times to twice. The most obvious variation is in the xiphiplastral points, which are found to range from distinctly concavo-convex to convex on both lateral and mesial margins.

The bases of the inguinal buttresses cover more of the plastron's width than do the axillaries, but the latter are well developed. The axillaries extend from 20 to 40 per cent of the way from the axillary notch to the mid-line, and the inguinals extend from 40 to 60 per cent. The inguinals are in all cases observed along the suture between pleurals 5 and 6, being mostly on pleural 5. They rise in adults to within 2 cm. of the rib-head on pleural 5. The axillaries in every case are fused to pleural 1, and form a continuous ridge with its rib-head.

The nuchal bone varies greatly in width, particularly in the *obscura* type, in which the length is 130 per cent of the greatest width. The minimum ratio is 68 per cent. The mean is 85 per cent, which would probably be close to the "normal" maximum were the *obscura* type excepted.

The first neural bone is consistently oval or sub-rectangular. Neurals 2 through 7 are regularly hexagonal, with the wide ends facing forward. In the series, the widths show no pattern at all; the widest may be any one from neural 2 to neural 7. There is more regularity in the lengths, however. The third neural is almost always the longest of the hexagonal ones, and the next longest is usually the fourth, but may be the second

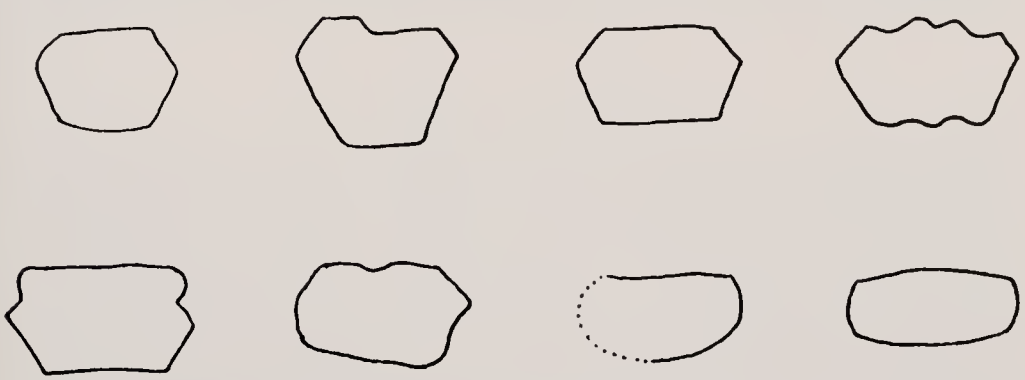

Fig. 5. *Echmatemys septaria callopyge.* Variation in shape of eighth neural bone.

or fifth. The most common order from longest to shortest is 3-4-2-5-6-7-8. The eighth neural varies greatly in shape, but is no doubt to be considered basically hexagonal like the others (Figure 5).

The first vertebral scute, as mentioned above, is inconstant in proportions, with that of the type being the narrowest (length 139 per cent of width). The range of the same ratio in other specimens is from 84 to 127 per cent. The second vertebral scute appears to be always more or less urn-shaped, with its lateral borders distinctly curved. In some cases, the length on the mid-line and greatest width are about equal, but mostly the scute is up to 25 per cent wider than long. The third vertebral is also urn-shaped, but its lateral margins, while having the shape of brackets, are straighter than those of the scute in front of it. It oftener has the length and width about equal; the mean length/width ratio is 1.04.

Two of the specimens studied have extra components. The supernumerary costal scutes of the *hollandi* type are discussed above. A fragment from the Wampus Cat quarry shows the suture of an extra posterior peripheral bone which occupies portions of the pygal and its contiguous peripheral on the left side (Figure 6).

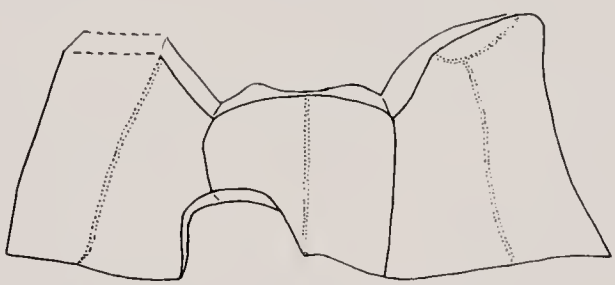

Fig. 6. *Echmatemys septaria callopyge*. Diagram of pygal and posterior peripherals, showing suture for supernumerary peripheral (MCZ 3145).

Growth Pattern

Fortunately, several immature specimens have been collected, and while they are in most cases rather incomplete, the growth pattern is indicated in three respects. Taking the type as an example of a full-grown mature individual, the smallest shell is about ⅓ the adult size. The Uinta fossils have been compared with a series of *Chrysemys picta marginata* from Cuyahoga Co., Ohio, in the Cleveland Museum collection, and a comparison is shown in Table II. Naturally, the vertebral scutes become

relatively narrower in both species with advancing age. In *Chrysemys*, the epiplastral lip lengthens slightly in the growth series, but the figures on *Echmatemys s. callopyge* are inconclusive. They suggest that the development of the lip is the same in young individuals as it is in old ones (Figure 7). In *Chrysemys*, the anterior lobe lengthens greatly relative to its basal width as the animal grows; the proportions in *E. s. callopyge* appear to change in the same direction, but to a lesser degree.

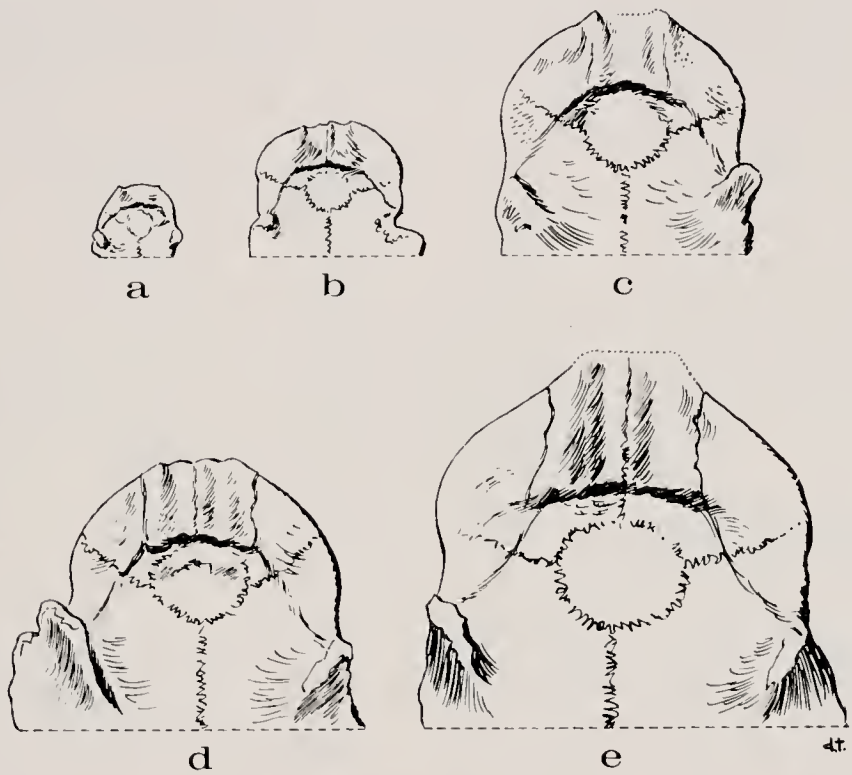

Fig. 7. *Echmatemys septaria callopyge*. Growth series. *a*, MCZ 3149, smallest specimen collected; *b*, MCZ 3133; *c*, CLM 10919; *d*, MCZ 3138; *e*, MCZ 3128 (x ¼).

In young individuals of the Uinta subspecies, the shapes of the vertebral scutes and particularly the configuration of the anterior lobe of the plastron bear the stamp of *callopyge*, and are readily identifiable. The scutes, of course, are less mature in their development in that they are considerably wider than long. The smallest specimen studied (MCZ 3149) exhibits a well developed epiplastral lip. The ratio of lip length to length of hyoplastron at the mid-line (.47) is within the range of variation of adults, and the ratio of lip length to anterior lobe length

(.35) is only slightly below the adult minimum. In comparison, an *Echmatemys* cf. *wyomingensis* shell of similar size (AMNH 6153) furnishes corresponding ratios of .18 and .16.

In the specimen MCZ 3149, the entoplastron is diamond shaped instead of pear shaped; whether this is an individual variation or an indication of youth is unknown.

Limbs, Girdles, and Vertebrae

A small number of bones of the appendicular and axial skeletons have been collected, the bulk of which belong with specimens MCZ 3125 and CLM 10627, or come from the matrix of

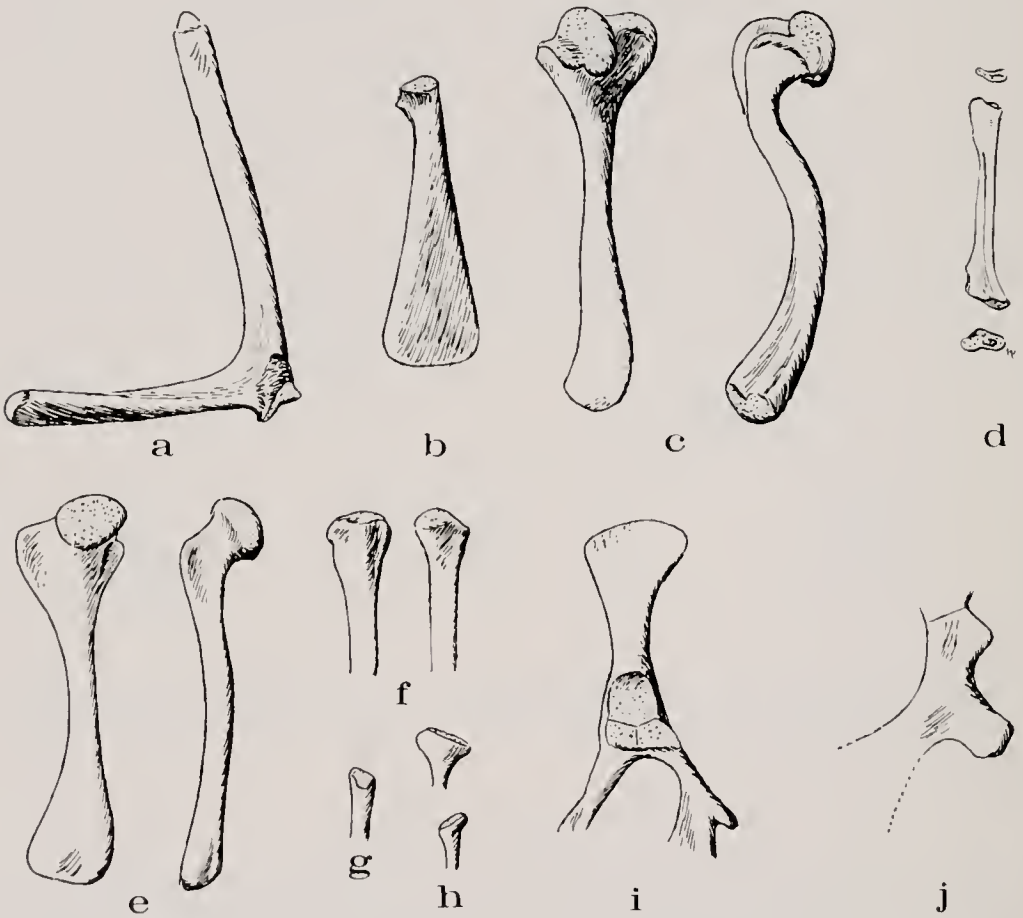

Fig. 8. *Echmatemys septaria callopyge.* Limb and girdle elements. *a*, left scapula (MCZ 3125); *b*, left coracoid (MCZ 3125); *c*, left humerus (MCZ 3147); *d*, right radius (MCZ 3126); *e*, left femur (MCZ 3125); *f*, left tibia (MCZ 3125); *g*, presumed proximal end of left fibula (MCZ 3125); *h*, sacral rib (MCZ 3125); *i*, right pelvis, restored from MCZ 3125 and 3129, and CLM 10627; *j*, upper side of left pubis, restored from MCZ 3125 and CLM 10627 (x ½).

the Wampus Cat quarry. The femur, humerus, radius, and pectoral girdle have been completely preserved, and the pelvis can be restored except for the distal portions of the pubis and isehium. Partial tibiae, fibulae, and ulnae have been found, as well as sacral ribs, some caudal vertebrae, and two cervical vertebrae. Not a scrap of skull or jaw has turned up.

These elements compare well with their counterparts in the Painted Turtle, *Chrysemys picta*. The ratios of limb bone lengths to plastron lengths are similar in both, as are the basic shapes. These facts plus the relative delicateness of the limb bones show that the legs of *Echmatemys septaria callopyge* were no better developed than are those of the modern Painted Turtle.

One of the cervical vertebrae is most probably a fourth; it appears to be narrower anteriorly than the fourth in *Chrysemys*, but otherwise resembles it. The other cervical is a characteristic eighth.

Hay (1908, p. 297) illustrated a series of limb and girdle bones presumed to pertain to *Echmatemys*. The similarities between these and the *E. s. callopyge* material are obvious, and the differences are minor. In view of the paucity of such fossils, I see no reason for a detailed comparison at this time.

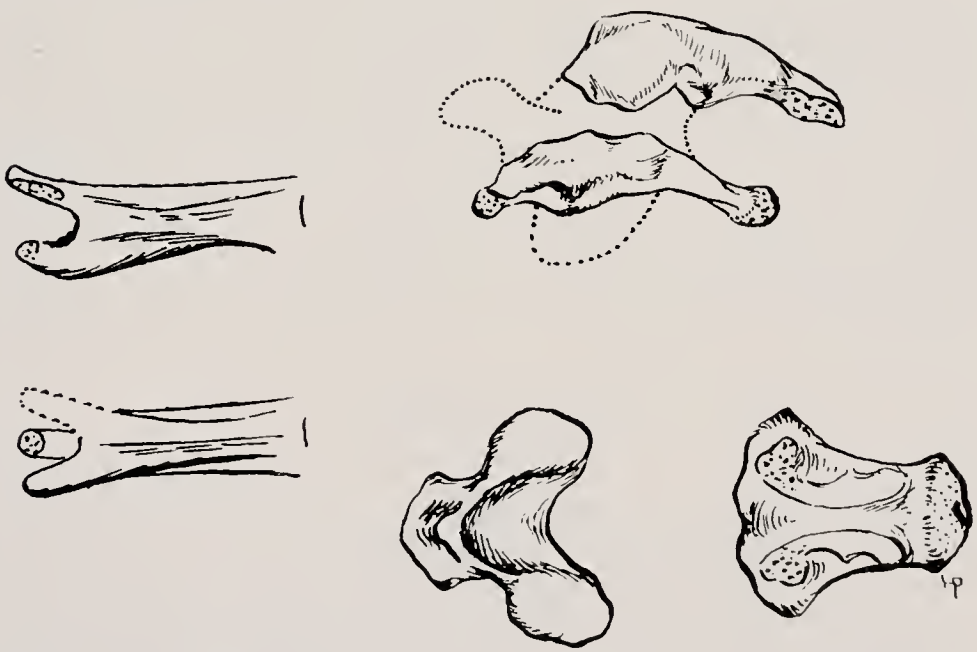

Fig. 9. *Echmatemys septaria callopyge*. Cervical vertebrae. Left: fourth cervical, right side and top view (MCZ 3129). Right: eighth cervical, left side (ventral process and sides of neural canal broken away) and top views of neural arch and centrum (MCZ 3126) (x 1).

It can be said that the known skeletal elements of *E. s. callopygc* are not unusual for an emydine turtle, and match those of Recent pond turtles. The anatomy of the Uinta subspecies herein described plus the petrology of the Wampus Cat quarry lead to the conclusion that *callopygc* probably matched in appearance and habitat the Painted Turtle of today, although, of course, it was much larger.

ACKNOWLEDGEMENTS

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BIBLIOGRAPHY

Cope, E. D.

1873. On the extinct Vertebrata of the Eocene of Wyoming, observed by the expedition of 1872, with notes on the geology. Annual Report, U. S. Geol. Surv. Territories, **6**: 545-649.

1882. The reptiles of the American Eocene. Amer. Nat., **16**: 979-993.

1884. The Vertebrata of the Tertiary formations of the West. Book I. Rept. U. S. Geol. Surv. Territories: 1-1009.

Hay, O. P.

1902. Bibliography and catalogue of the fossil Vertebrata of North America. U. S. Geol. Surv. Bull., **179**: 1-868.

1906. Descriptions of two new genera (*Echmatemys* and *Xenochelys*) and two new species (*Xenochelys formosa* and *Terrapene putnami*) of fossil turtles. Bull. Amer. Mus. Nat. Hist., **22**: 27-31.

1908. The fossil turtles of North America. Carnegie Institution of Washington, Publ. no. 75: 1-555.

GILMORE, C. W.

1915. The fossil turtles of the Uinta formation. Mem. Carnegie Mus., **7**(2): 101-162.

1945. A slab of fossil turtles from the Eocene of Wyoming, with notes on the genus *Echmatemys*. Amer. Jour. Sci., **243**(2): 102-107.

TABLE I

PROPORTIONS OF CARAPACE AND PLASTRON IN ADULTS

		Max.	*Min.*	*Mean*	*No. of Measurements*
Length epiplastral lip on mid-line/ overall length of plastron					
	callopyge	.14	.10	.12	11
	septaria	.10	.09	.09	5
Length epiplastral lip on mid-line/ length anterior lobe					
	callopyge	.50	.36	.40	18
	septaria	.36	.27	.32	9
Length epiplastral lip on mid-line/ length hyoplastron where it reaches the mid-line					
	callopyge	.71	.43	.58	17
	septaria	.49	.35	.41	9
Width anterior lobe at base/length anterior lobe on mid-line					
	callopyge	1.61	1.24	1.43	21
	septaria	1.58	1.30	1.45	10
Width anterior lobe at base/overall length of plastron					
	callopyge	.50	.38	.43	22
	septaria	.48	.38	.42	7
Distance between epiplastral teeth/ width anterior lobe at base					
	callopyge	.40	.20	.28	21
	septaria	.36	.22	.28	9

TABLE I (Cont.)

		Max.	*Min.*	*Mean*	*No. of Measurements*
Width posterior lobe at base/ greatest length posterior lobe					
	callopyge	2.10	1.16	1.44	14
	septaria	1.50	1.25	1.33	7
Second neural: length on mid-line/ greatest width					
	callopyge	1.21	.90	1.02	15
	septaria	1.22	.97	1.10	9
Fourth neural: length on mid-line/ greatest width					
	callopyge	1.36	.95	1.11	17
	septaria	1.37	.97	1.10	8
First vertebral: length on mid-line/ width in middle					
	callopyge	1.39	.81	1.10	22
	septaria	1.05	.74	.87	8
Second vertebral: length on mid-line/width in middle					
	callopyge	1.03	.63	.88	23
	septaria	1.25	.98	1.09	8
Third vertebral: length on mid-line/ width in middle					
	callopyge	1.22	.83	1.04	17
	septaria	1.22	1.03	1.12	8
Nuchal bone: length on mid-line/ greatest width					
	callopyge	1.30	.68	.85	7
	septaria	.85	.63	.73	8
Length entoplastron/greatest width entoplastron					
	callopyge	1.08	.91	1.02	19
	septaria	.98	.73	.88	10
% of lobe base occupied by buttress					
	callopyge				
	axillary	40	17	29	15
	inguinal	60	40	56	12
	septaria				
	axillary	39	29	34	2
	inguinal	53	40	48	3

Table II

Growth Series

		A	B	C	D	E
Chrysemys picta marginata						
CLM ZF	1492	2.3	.043	5.0	.33	.33
	1490	7.2	.056	2.2	.52	.50
	251	9.7	.062	1.9	.66	.61
	1302	14.0	.064	1.8	.70	.66
Echmatemys septaria callopyge						
MCZ	3159	9.0*	——	1.7	.59	.66
	3132	16.7	.123	1.8	.68	.82
	3125	39.0	.136	1.5	.82	1.00
AMNH	2087	42.0	.114	1.5	1.01	1.06

A—Overall length of plastron in centimeters
B—Length of epiplastral lip on mid-line/length of plastron
C—Width anterior lobe at base/length anterior lobe on mid-line
D—Second vertebral — length/width
E—Third vertebral — length/width
* Estimated

Table III

Epiplastral Lip Development in Emydines

Length of epiplastral lip on mid-line/overall length of plastron

Species	*Ratio*	*No. of Specimens*	*Catalog Nos.*
Graptemys sp.	.01	1	**
Pseudemys scripta cataspila	.03	7	MCZ 46389-91, 46394-96, 46398
Echmatemys wyomingensis	.04	1	CLM 10181
Terrapene carolina	.05	2	CLM ZF 1240, **
Chrysemys picta marginata	.06, .07	2	CLM ZF 1302, **
Emydoidea blandingii	.06, .07	2	CLM ZF 839, **
Clemmys insculpta	.07	1	CLM ZF 477
Echmatemys uintensis	.05, .08	2	UFH 214, 223
Echmatemys douglassi	.08	1	UFH 205
Pseudemys scripta scripta	.08	1	CLM ZF 484
Clemmys guttata	.09	1	CLM ZF 506
Echmatemys septaria septaria	.09–.10	5	
Echmatemys septaria callopyge	.10–.14	11	

** Specimen belonging to the author

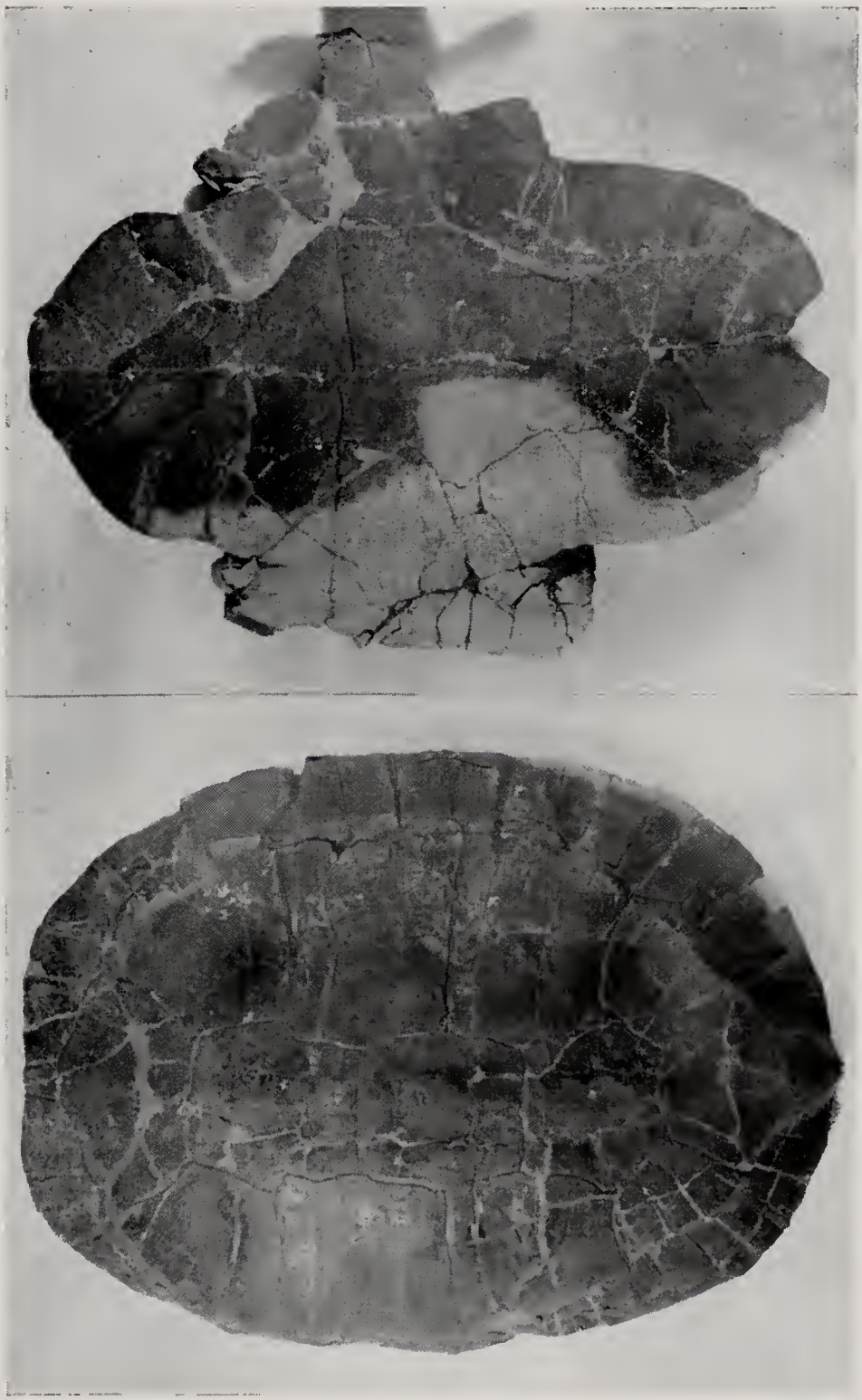

Plate 1. *Echmatemys septaria septaria.* External views of plastron and carapace of referred specimen (USNM 16687) (x 3/10).

Plate 2. *Echmatemys septaria callopygc.* External views of plastron and carapace of typical individual (MCZ 3125) (x ¼).

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BEHAVIOR OF *DACETON ARMIGERUM* (LATREILLE), WITH A CLASSIFICATION OF SELF-GROOMING MOVEMENTS IN ANTS

By

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CAMBRIDGE, MASS., U.S.A.
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No. 7 — Behavior of Daceton armigerum *(Latreille), with a classification of self-grooming movements in ants.*

By Edward O. Wilson

INTRODUCTION

The Neotropical ant species *Daceton armigerum* is the only member of its genus and the largest and most primitive representative of the great predaceous tribe Dacetini (Brown and Wilson, 1960). Unlike most dacetines, it is completely arboreal. Further, its worker caste exhibits polymorphism of the greatest magnitude found in the Dacetini and one of the most extreme for ants generally. The combination of these characteristics makes it a strikingly discrete entity within the Neotropical ant fauna.

To date only a few fragments of information on the biology of this significant species have been published. As noted in a recent review of the Dacetini (Brown and Wilson, 1960), it has been collected chiefly from forested localities in the Amazon-Orinoco Basin of South America. A single nest has been found in the trunk of an unidentified tree at Itacoatiara, Brazil (Mann, 1916). On several occasions workers have been discovered foraging during the day. Very limited prey records suggested that the species is generally insectivorous, although the point was far from proven. Until the present study, no nest had been dissected, and details of behavior were unknown.

During field work in Surinam in March, 1961, I made a special attempt to locate and study the species. A single colony was captured and kept under observation in an artificial nest for two months. In April, by a stroke of good luck, a second colony was located in Trinidad, thus yielding the first record of the genus from the West Indies. The Trinidad colony was not recovered from the nest tree, but proved very useful for field studies of foraging behavior.

ECOLOGY

Habitat. Although *Daceton* has been previously considered exclusively a rain-forest dweller, neither of the study colonies came from this environment. One was located in primary swamp forest directly north of the Government Botanical Gardens (Landboewprufstation) at the outskirts of Paramaribo, Surinam. The forest, of uniform facies, extended unbroken from

Unfortunately, the discovery was made too late to allow time for the tree to be felled and opened.

Colony composition. The Paramaribo colony, as noted, was in a mature state (containing alate queens), so that an estimate of its size is of special interest. After the nest had been dissected, the following numbers of adults were totalled from the live colony in the artificial nest and preserved material: one dealate queen, three alate queens, two males, 270 ± 20 workers. A few workers were left foraging or lost during collection. The total number of workers in the colony, including foragers, probably fell within the limits of 280-320.

No census was made of the Trinidad colony. Nevertheless, casual inspection showed that it was much larger than the Surinam colony. On April 13, 218 workers were collected and preserved on foliage away from the host tree without greatly reducing the foraging population. On April 27, what appeared to be the entire trophophoric field was scanned, and the number of foraging workers was roughly estimated to be in excess of a thousand. In Surinam the ratio of diurnal foragers to nest inhabitants was estimated to lie between 1:10 and 1:5. If the same ratio obtained in the Trinidad colony, the total worker population may have ranged as high as 5,000 or even 10,000. But these latter figures have only the weakest conjectural significance until more *Daceton* colonies are collected.

Foraging area and diet. The *Daceton* workers forage extensively during the day. On April 13 I remained at the Cumuto, Trinidad, locality until dusk, at which time a significant decrease in activity was noted. The nest sites were not visited at night.

Foraging appeared to be limited exclusively to arboreal vegetation but was not devoted preferentially to any part of the vegetation. Workers moved up and down tree trunks, across trees on lianas or at the points of interlacing crown vegetation, onto epiphytes, and out to the very tips of branches, twigs, and leaves. Seedlings only a meter or two in height were visited as well as the tallest trees. At Paramaribo, workers were noted on the trunks of four trees, the more distant approximately 14 meters from the trunk of the nest tree. At Cumuto workers ranged maximally to between 16 and 20 meters from the assumed nest tree. Dead as well as live foliage was visited. At Cumuto, workers were abundant in the crown of a felled "galba" tree, *Calophyllum brasiliense,* from which most of the leaves had already fallen. Evidently, *Daceton* workers do not normally forage on the ground. At neither locality was a single worker seen

there. Workers were followed repeatedly as they neared the ground; some proceeded to the base of the trunk or onto the buttresses, but none went further.

Before the present study, only two records of *Daceton* prey had been published: a tabanid fly and an acridid grasshopper (Brown and Wilson, 1960). In the following list are all of the additional natural prey recorded at Cumuto during the afternoons of April 10, 13, and 27, along with their approximate length: Seven moth larvae (3, 5, 8, 8, and 23 mm; two were not measured); one adult moth; two adult curculionine weevils (both 5 mm); one adult cryptorhynchine weevil (3 mm); one beetle larva (8 mm); one fulgorid (7 mm). All were being carried by single workers, except the 23-mm moth larva which was being hurried along by four workers running together. All of the prey appeared to have been freshly killed, presumably by the *Daceton*. Of all the workers seen running nestward, only a very small fraction, about 1 or 2 per cent, were laden with prey. Foraging workers that were offered freshly killed polybiine wasp workers accepted these readily and carried them homeward. In the artificial nest, the Surinam colony consistently accepted flies (Muscidae, Psychodidae, Sarcophagidae, Tabanidae, Tachinidae, etc.) and usually accepted acridid grasshoppers. On the other hand, they rejected (after killing) a coccinellid beetle, a coccid, several cicadellids, and a honeybee (*Apis*). The significance of this apparent selectiveness, contrasting as it does with the obvious catholicity of prey choice of the wild Trinidad colony, remains to be explained. Workers also commonly consumed brood in the artificial nest; this may have been an abnormal reaction.

It should be noted that while *Daceton* is generally insectivorous, or at least nearly so, the size range of its prey is not very great. For this reason, the two colonies did not have serious competition from other ant species penetrating their trophophoric fields. Only the *Neoponera* at Cumuto could readily capture prey in the size range preferred by *Daceton*, and these ants were represented by a single small colony. The ants that seemed to create maximum interference, on the other hand, were the *Azteca*. At both localities species of this dolichoderine genus were by far the most abundant ants present. They were quite aggressive and were frequently observed attempting to seize the legs of the *Daceton*, especially when the nests were disturbed by the human observer. But the size difference was too great to allow serious interference. The *Daceton* moved through the *Azteca* swarms like elephants through crowds of pygmies.

According to Bodkin (in Crawley, 1916), *Daceton* workers were observed attending coccids in British Guiana. No evidence of nectar or honey-dew gathering was found during the present study. However, workers in the artificial nest fed eagerly on sugar water and exchanged the fluid freely among themselves by regurgitation.

BEHAVIOR

Hunting and nest defense. Daceton workers observed in the field at Cumuto explored the foraging area singly. There was no evidence whatever, either in the field or in laboratory, of trail laying or other special forms of recruitment following discovery of food. In the artificial nest, workers often moved toward areas of excitement, evidently stimulated by other workers when prey were being chased or captured, and this response can be interpreted as a very low level of communication. The ants did not seem to react to movements more than ten millimeters from their heads. The orienting stimuli were at least partly visual, since workers reacted similarly to movement in the area directly outside the transparent walls and cover of the nest. (A description of the type of artificial nest used is given in Wilson, 1962.)

Foraging workers remained nearly constantly in motion, ambling along at a pace proportionate to size that was closer to foraging *Tetramorium* than to the more sluggish higher Dacetini. The mandibles were almost always held partly open, making an angle of between 45° and 90°. Both the surface of the foliage and crevices were explored by antennation. The ants often paused to lift the head slightly and wave the antennae in the air briefly. Resting workers did not appear to be engaged in "ambush hunting." Workers most frequently paused where other workers were resting, and this was typically in crevices and other sheltered places. At such times the mandibles were not held in striking position, nor was there any other aspect of the posture to suggest that the ants were set to ambush prey. A unique feature of *Daceton* morphology is the ability in the worker to swing the head upwards and backwards so that its long axis forms a right angle or less with the remainder of the body. Thus a worker has the capacity to point the head vertically from the surface on which it stands. It has been a point of guarded conjecture among myrmecologists that such a posture might be used in ambushing insects. Yet no such posture was ever seen to be taken during the course of normal foraging.

Nor was such a posture ever assumed during the many captures of insect prey observed in the artificial nest. The adaptive significance of the hinged head may lie in an entirely different behavioral category, that of food exchange (*vide infra*).

Slight disturbance caused the workers promptly to open and lock the mandibles at maximum extension, so that their inner borders formed an angle of approximately 170° (see Figure 1). Foraging workers in the field clearly were very perceptive visually to movement. They wheeled about quickly to face any moving object. If the object was a large one, such as a human hand, the ants darted in reverse, revealing the curious ability to run backward as rapidly as forward. Slight movement, which must

Figure 1. Media worker in stalking posture. Drawn from a single 16-mm frame of a motion picture of the Surinam colony.

be close to the ant, induced a cautious movement toward the object. At such times the mandibles were always locked open, the scapes aligned along the mandibles, and the funiculi pointed straight ahead. If the object were acceptable prey, little time was spent in the approach. In the field the ants walked toward the dead insects offered them (polybiine wasps) deliberately and slowly for periods lasting no more than five seconds, then struck with the mandibles. The stalk resembled that of *Strumigenys louisianae* (Wilson, 1953) but was more abrupt. Sometimes it was eliminated altogether, with the ant briefly antennating the prey before striking. In the artificial nest, living

prey were often chased by the *Daceton,* which seemed to lose perception of them at distances greater than about ten millimeters. The act of chasing for considerable distances sets the hunting behavior of *Daceton* distinctly apart from that of other dacetines studied. It is evidently afforded by the exceptional vision provided by the large eyes of these insects.

The mandibular strike, as in higher dacetines, was convulsive and severe. It drove the sharp apical teeth deeply into the bodies of softer insects and was adequate even to force the points into the softer skin of the author's hand. Following the strike, the prey was lifted slightly from the ground with a barely visible upward movement of the head. Exceptionally long tarsal claws anchored the ant firmly to the bark surface and aided it in holding on to large or vigorous prey. On the field, when prey carried by *Daceton* workers were seized by a pair of forceps and pulled, the ant hung on tenaciously and could be torn loose from the bark only with difficulty; sometimes the prey was pulled asunder in the process. Following the mandibular strike, the ant often made a very short backward run; occasionally it paused for a while, grasping the prey firmly. The sting, when it was administered, involved the same movements already described in *Strumigenys* (cf. Brown and Wilson, 1960). Workers encountering prey being carried by other workers repeated or attempted to repeat the hunting sequence on their own. The result is that large or unusually vigorous insects could be subdued by the attacks of several ants, and sometimes more than one ant cooperated in carrying it home. Workers commonly pulled the prey from the mandibles of other workers, with the result that the largest workers generally ended up with the prey before it got all the way to the nest (see the later section entitled "Division of labor").

While I was collecting the Surinam colony, I was stung twice by large media workers (head width 3 mm), each time in the soft skin between the thumb and forefinger of the left hand. This event perhaps allows me to make the esoteric claim of being the first myrmecologist to be stung by a dacetine ant. The mandibular strike felt like the light jab of a needle, and this was quickly followed by a moderate, very localized burning sensation. An erythema quickly appeared around the point of sting entry, spreading within several minutes to form a circular patch approximately 30 millimeters in diameter. At the same time a welt 5 to 8 mm wide was raised in the center. At maximum development the inflammation caused moderate burning

and itching, very similar to that caused by an allergenic mosquito bite. The effect gradually subsided, and thirty minutes after the sting only a faint erythema remained. The symptoms closely resembled the superficial effects of the sting of certain other myrmicine ants such as fire ants of the genus *Solenopsis,* rather than the deeper, throbbing, fluctuating pain caused by ponerine ant and certain wasp stings.

The nests were defended by aggressive behavior similar in all details to that seen during hunting, save that the ants were more excited and precipitous in their movements. Insects invading the nest but rejected as prey were killed in the same manner as prey, but later were ejected from the nest.

Self-grooming. In describing self-grooming behavior of *Daceton* systematically, attention will be focused on an interesting and promising subject in myrmecology mostly neglected since the time of McCook (1878). Self-grooming involves complex movements which are among the most stereotyped in all the ants' repertory. My own notes on a wide range of genera confirm that self-grooming behavior varies widely within the Formicidae and thus offers excellent new characters for evolutionary studies. It can be further noted that it is not the basic movements themselves that vary greatly, but rather the pattern of their presence or absence. This characteristic provides the excellent opportunity to construct grooming "formulas" for inclusion in taxonomic descriptions. In the short sections to follow are given descriptions of the basic movements used by *Daceton,* plus movements I have observed in other ant groups but not in *Daceton.*

Self-grooming Movements Used by *Daceton armigerum* Workers

(1) Oral "leg" cleaning. The front tarsi and distal parts of the tibiae are drawn, one after the other, over the lower mouthparts and glossated in the process. This is perhaps the most basic and important self-grooming movement, since it transfers detritus picked up in the strigils of the tibial spurs to the mouthparts, whence it is transferred to the infrabuccal pocket for later discharge as a pellet. All ant species studied by me employ this movement. *Daceton* is unusual in that both front legs are lifted off the ground simultaneously during the movement.

(2) Antenna wiping. The antennae are wiped with the strigils of the fore-tarsal spur. This movement appears to be universal in the Formicidae. As in (1), *Daceton* is unusual in typically holding both front tarsi simultaneously off the ground during the movement.

(3) Normal four-leg wiping. This term might be conveniently applied to the complex movement, apparently universal in ants, in which the body is supported on a tripod consisting of the tip of the gaster and middle and hind legs of one side, while the fore leg of the first side and three legs of the opposite side are wiped together. An aberrant variation is no. 13, four-leg wiping (front-middle) (*vide infra*).

Movements (4) and (5) below can be interpreted as transitional to (3):

(4) Three-leg wiping (front-middle). Similar to four-leg wiping but involving only the two front legs together with the middle leg on one side. Not found in all ant taxa.

(5) Two-front-leg wiping. Involving only the two front legs. Not found in all ant taxa.

(6) Abdominal tip cleaning. The gaster is bent forward between the legs and its tip washed with the lower mouth parts. Found in most, but not all, ant taxa.

(7) Head wiping. The front tarsi are drawn over the sides of the head. An irregular movement not found in all ant taxa. In some other taxa the top of the head is stroked as well.

(8) Abdomen wiping (front legs). The abdomen is bent forward between the legs and the sides stroked briefly and irregularly with the front legs. Accompanies (6). An unusual act for ants generally and seen only twice in the *Daceton* study.

Self-grooming Movements Used by the *Daceton* Queen and Male

The mother queen was observed using movements 1 through 7 above, thus duplicating the worker repertory almost in its entirety. Movement 8 was not seen, but the significance of its omission is uncertain due to its rarity in the worker caste. During a brief observation period males were observed using movements 1 through 5; this is probably not their complete repertory.

Self-grooming Movements Observed in Other Ant Taxa but not in *Daceton*

(9) Abdomen wiping (hind legs). Similar to (8), but the abdomen is held straight and the hind legs are used. The dorsal surface of the gaster may also be stroked. Typical of more primitive taxa.

(10) Metapleuron wiping. The front legs are folded back and rubbed against the metapleura in a sawing motion.

(11) Two-hind-leg wiping. The abdomen is lifted slightly and the two hind legs are stroked together. Typical of some primitive taxa.

(12) Three-leg wiping (hind-middle). In the formicine *Gigantiops destructor* (Fab.) the following unusual movement has been observed: the abdomen is lifted slightly, the hind legs are held rigidly off the ground and pressed together, and one of the middle legs is stroked against the ipsilateral hind leg.

(13) Four-leg wiping (front-middle). In queens of the myrmicine *Erebomyrma urichi* (Wheeler) the two front and two middle legs are sometimes wiped together simultaneously.

Other grooming. As in other ant species, the workers glossated one another, other castes, and the brood frequently. This was the most frequent social act. The mother queen was once observed glossating a callow worker, but she obviously engaged in other-grooming far less commonly than individual workers.

Brood care. Brood in all stages of development were mixed together in irregular piles in the nest. Nurse workers constantly manipulated the brood with their fore tarsi as they washed them, thus alternately burying and bringing to the surface immature individuals. Newly hatched larvae were left for a while with the eggs and were apparently fed by the workers exclusively by regurgitation. The possibility that some larvae, especially young larvae, also fed on queen-laid eggs cannot be excluded on the basis of my own limited observations. No worker was ever seen to lay an egg; it is at least certain that worker-laid "trophic eggs," if they were produced at all, did not play any role of significance in larval and queen nutrition, as they do in some other ant species [e.g., *Pogonomyrmex badius* (Latreille)]. Larger larvae were fed frequently by regurgitation. They were also given fresh pieces of prey placed directly on their heads. Small larvae (but not newly hatched ones) were sometimes placed on top of the prey. The larvae were evidently fed in a manner similar to what Brian (1956) has appropriately termed the "test-servicing" system in the genus *Myrmica*. Workers were sometimes seen to move from larva to larva, extending their glossae in the feeding motion to each, without eliciting a feeding response.

Brood transport poses a special problem for the *Daceton* workers because the sharp apical teeth of their predatory mandibles might easily break the skin of immature forms, especially the larger larvae. It may be noted in passing that the workers of

the related genus *Acanthognathus* have the same problem and a novel device for solving it: a pair of small teeth near the base of the mandibles are used to grip and carry brood, thus bypassing the apical teeth (Mann, 1922; later confirmed by W. L. Brown, *in litt.*, 1961). The *Daceton* also have a peculiar solution. When highly excited, as when the nest was first broken open, they used the apical teeth and were able to transport brood rapidly in this manner. But in leisurely emigration from one chamber to another in the artificial nest, workers almost invariably moved brood by tucking it under the head with the front legs and wrestling it backward!

Queen and male care. The mother queen and males were apparently fed exclusively by worker regurgitation. In two months of observation the queen was never seen to feed directly on prey, although it was constantly available.

When first captured and transferred to the artificial nest, the queen was closely attended by crowds of workers. As many as 14 touched her simultaneously, directing their heads to her body. When she moved she was invariably followed by a retinue of one to eight workers. Attending workers typically extended their lower mouthparts far enough to allow the maxillary and labial palps to play over the queen's body surface. One worker, always one of the majors or large medias, assumed the posture of "footman" during the queen's movements: it followed directly behind her, its front legs and fore part of its body resting on her gaster and the middle and hind legs and rear part of the body running awkwardly behind. Later, as the colony declined, the queen received increasingly less attention and finally lost her retinue altogether, including the remarkable "footman."

Regurgitation. Transfer of liquid food by regurgitation was a very common event in the captive Surinam colony. When the colony contained approximately 200 workers, one could find one or two pairs, or 1 to 2 per cent of the worker population, engaged in regurgitation most of the time. On several occasions when sugar water was given after being withheld for two or three days, the percentage of simultaneous regurgitating workers increased conspicuously, to as high as 10 per cent. Mature workers regurgitated more to callow workers and larger workers to minimae than vice versa, at least at first, but otherwise there was no visible structure with reference to castes in the exchange pattern. Minors gave freely to minors, majors to majors, majors to minors, minors to majors, etc., in what seemed to be every

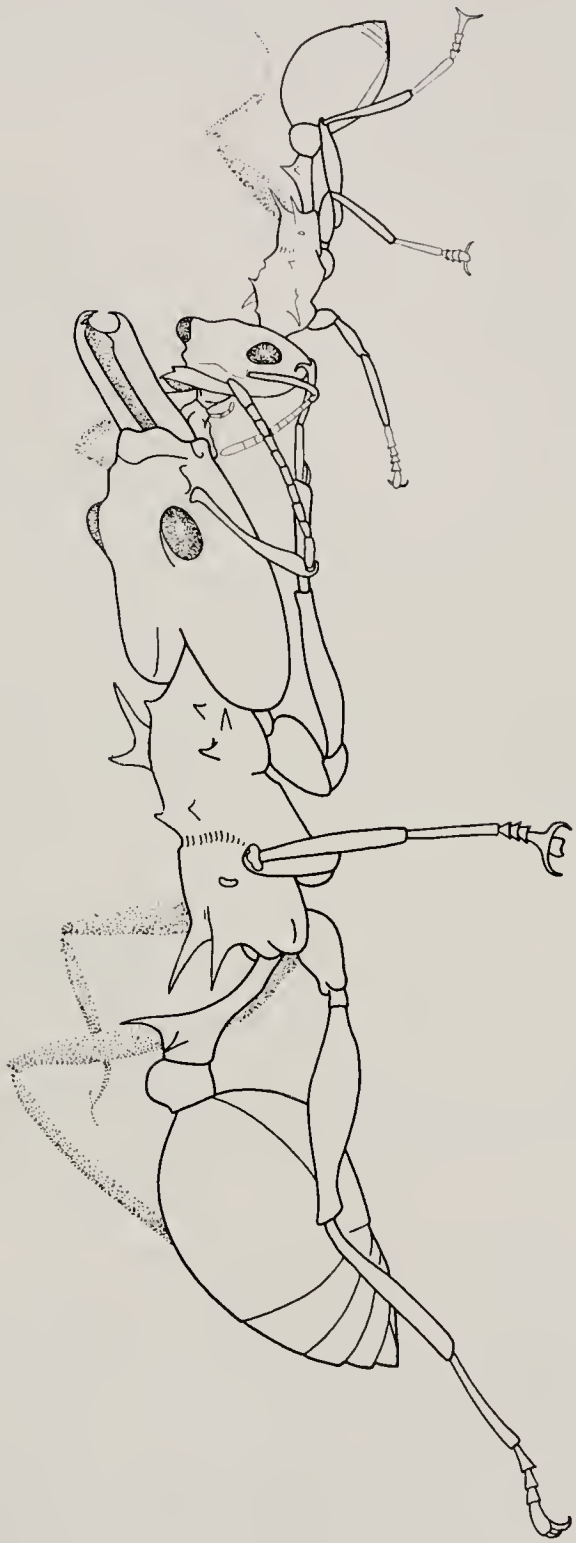

Figure 2. Minor worker regurgitating to large media. The recipient grasps the head of the donor with its fore tarsi, while both individuals slowly antennate the vicinity of the passing ingluvium. In this case the head of the donor is tilted upward in the posture peculiar to *Daceton*. Drawn from a single 16-mm frame of a motion picture of the Surinam colony.

possible combination. After they had received sugar water in this manner, the callows and minimas confined too closely to the brood area to feed directly on the food, donated it readily among themselves and to others. There may, however, have been differences in the frequencies of exchange too subtle to detect without extensive measurements.

During liquid exchange both partners held the mandibles closed or nearly so. The donor usually held its body straight or leaned slightly to one side. Its head and thorax were tilted upward, and the head was often turned more radically upward to form as much as a right angle with the thorax. In a minority of cases, the donor placed its front tarsi on the head of the recipient, and it usually antennated the head of the recipient rapidly during the exchange. The recipient typically twisted its body more strongly than the donor, sometimes as much as 45° from the ground level. If its body was held straight, it usually turned the head up to a right angle with the thorax to touch mouthparts with the donor in the same position. Thus the unique head-lifting posture of *Daceton* workers appears to be used chiefly to facilitate food exchange. During transmission the recipient almost always placed its front tarsi on the head of the donor and antennated its head rapidly. Occasionally two workers received simultaneously from the same donor, forming with it a "tripod" of bodies. (See Figure 2).

Adult transport. The carrying of adults by other adults was conspicuously absent. In numerous emigrations observed following dissection of the Surinam nest and later in the artificial nests, all adult members moved on their own. Only once was a worker observed carrying a newly eclosed callow worker over a brood pile in the artificial nest. It treated its burden much like a pupa, gripping it awkwardly by the thorax and legs. Even true brood was rarely lifted with the mandibles (see under "Brood care").

Egg-laying. The mother queen was observed once in the act of oviposition. She held her body straight. When first observed the egg was already one-third extruded; then it was totally retracted; finally, about 30 seconds later, it was totally extruded and stuck onto the nest ceiling, where the queen hung suspended. Immediately after the egg was detached, the queen walked slowly away, paying no further attention to it. The egg was soon thereafter approached by a minima worker, who commenced washing it and pulling at it with its front tarsi.

Division of labor. The total range of head width of workers in the Surinam colony was 1.2-4.6 mm. The head width of living workers in the artificial nest could be measured with reasonable certainty to the nearest two-tenths of a millimeter. For convenience, workers were classified according to the nearest millimeter of head width, thus dividing them into four arbitrary classes: "minor," including the smallest "minimas," (1 mm), "small media" (2 mm), "large media" (3 mm), "major" (4 mm). Only one individual was found with head width as great as 4.6 mm and thus was classified as 4 mm. The method afforded little information about the size frequency distribution but was most useful in detecting the major features of polyethism. The results of the study are given in Table 1. Except for the small foraging sample, which was collected in the field, all of the measurements on the Surinam colony were made in the artificial nest between April 2 and April 10. All of the measurements on the Trinidad colony were made in the field, on April 13 and April 27.

TABLE 1

Division of labor among workers of *Daceton armigerum*

	Head width (mm)				Total no. of observations
	1	2	3	4	
Surinam colony:					
Total population (in artificial nest, April 5)[1]	13	60	20	9	102
Disposing of corpses and refuse[2]	0	19	12	2	33
Dismembering and feeding on fresh prey in nest[2]	0	14	25	5	44
Feeding larvae by regurgitation[2]	8	15[3]	3[3]	1[3]	27
Attending egg-microlarva pile[2]	24	3	0	0	27
Foraging in the field[1]	0	0	4	10	14
Trinidad colony:					
Foraging in the field[1]	1	91	77	12	181
Resting in way-station[1]	0	8	19	10	37
Carrying prey[1]	0	1	1	10	12

1Numbers refer to separate, individual workers.
2Numbers refer to separate behavioral acts, without regard to the number of workers engaged.
3Consisting mostly of callows ; see text.

These data allow some interesting conclusions. The *Dacetон* polyethism appears to approach most closely that of the formicine *Oecophylla longinoda* (Weber, 1949), but contains some unique features of its own. The smallest workers (head width 1.2-1.4 mm) remained constantly close to the brood and, despite their small numbers, were the principal custodians of the egg-microlarva pile and contributed heavily to the feeding of the larvae. They were assisted in the latter task by the callows of larger size classes. Thus, of the 15 times that small medias (head width 2 mm) were observed regurgitating to larvae, callows were involved in 7 cases, while of the larger castes only callows were seen engaged in this task. On one occasion a minor worker was seen cleaning a shed skin from a larva. Minor workers also freely regurgitated sugar water to other workers after they had received it by regurgitation themselves (see under "Regurgitation"). The minor workers were evidently limited to this simple repertory. They took virtually no part in hunting and dismembering of prey, refuse disposal, or nest defense. They seldom joined the queen's retinue.

Polyethism among the larger size classes (head width 2-4 mm) was less marked. Although measurements were not made, all seemed to partake equally in nest defense and in attending the queen. Large medias and majors (3-4 mm) were seemingly more prone to dismember and feed directly on fresh prey and more prone to serve as the queen's "footman" (see under "Queen and male care"), but distinctly less prone to feed larvae by regurgitation. Since the nest population of the Trinidad colony was not sampled, and the foraging sample of the Surinam colony was too small, it cannot be determined whether the medias or majors tend to forage more. But the Trinidad sample is sufficient in itself to reveal some finer polyethism with reference to the category of foraging behavior. A sample of workers, collected as they rested in a crevice of a tree trunk far removed from the nest, contained a significantly higher proportion of majors and larger medias than the sample of other foraging workers. Further, a strikingly high proportion of major workers occurred in the sample collected while carrying prey. The latter effect is perhaps due to the fact, mentioned previously, that workers constantly try to pull prey away from each other on the homeward journey. Very likely the major workers usually win in these struggles and arrive at the nest carrying prey which, in most cases, they have not captured themselves.

Mixing of colonies. It was discovered that foraging workers from the Trinidad colony could be introduced successfully into the captive Surinam colony. Fighting was rare and brief and resulted in no injuries.

DISCUSSION: THE PHYLOGENETIC POSITION OF *DACETON*

The new information on *Daceton armigerum* invites a second look at its evolutionary position. Like most "primitive" or linking taxa, *Daceton* exhibits a mosaic of primitive, intermediate, and specialized characters. Brown (1949) has pointed out that certain morphological characters, such as the antennal and palpal formulas, sculpturing, and pilosity, are quite generalized with reference to the Myrmicinae as a whole. The epigaeic foraging behavior is primitive for ants generally and certainly for the Dacetini, most of the higher members of which are conspicuously modified for cryptobiotic life (Brown and Wilson, 1960).

The hunting behavior is intermediate in development between the generalized myrmicine pattern and the peculiar higher dacetine pattern; that is, the mandibular strike is typically dacetine while the hurried approach and chasing behavior resemble more that of other myrmicine groups. Frequent regurgitation to larvae and other adults is a generalized characteristic, but the vertical head posture often assumed in regurgitation between adults is a unique development. The broad insect diet is primitive, as is the ready acceptance of sugar water and the rapidity with which it is distributed by regurgitation. *Daceton* is peculiar among the lower dacetines in its extreme adaptation to arboreal life, and in this regard it has probably deviated from the mainstream of early dacetine evolution. The extreme polymorphism and elaborate polyethism are probably also deviations.

The method of transporting brood with the forelegs is unusual, but higher dacetines have a similar tendency to use the forelegs skillfully. The absence of adult transport is unusual, although the behavior is shown by at least some higher dacetines. Details of self-grooming behavior are not sufficiently well known in other ant taxa to allow an evaluation of *Daceton* in this regard.

In conclusion, it is gratifying to be able to record that *Daceton* possesses some ecological and behavioral characteristics that are wholly primitive with respect to the rest of the Dacetini, just as was predicted in our earlier studies of dacetine evolution.

But there also exist a surprising number of striking specializations. One is tempted, in reliance on the convenient evolutionits's cliché, to place *Daceton* well down on the tribal tree but off to one side of the main stem. In our continuing search for the elusive dacetine prototype, we are forced now to turn to *Acanthognathus*, the little-known Neotropical genus most closely related to *Daceton*. This taxon, which is monomorphic and terrestrial, may prove on closer examination to form a more plausible link between the higher Dacetini and the remainder of the Myrmicinae.

SUMMARY

Biological notes are given on two colonies of *Daceton armigerum*, one from Paramaribo, Surinam, and the other from Cumuto, Trinidad. The latter comprises the first record of the genus from the West Indies. The nests were located in living trees in swamp forest (Surinam) and savanna forest (Trinidad). The Surinam nest was further determined to consist of abandoned beetle burrows in live branches. Estimates of colony size and composition are given. The workers preyed on a wide variety of insects 3-23 mm in length. Hunting and defensive behavior resembled that of *Strumigenys*, except that vision played an important role in orientation and the stalk was more hurried. Nest behavior of the Surinam colony is described in detail. A classification of the movements of self-grooming in *Daceton* and other ants is given. The workers exchanged liquid food freely among themselves by regurgitation; larvae were fed directly with pieces of prey and liquid food by regurgitation. Brood was normally transported about the nest by means of a peculiar wrestling movement involving the head and fore legs. Associated with the extreme polymorphism of the worker caste was an elaborate polyethism most closely resembling that of *Occophylla* but with features peculiar to *Daceton*.

The combination of generalized myrmicine characters in morphology and behavior with a number of striking specializations suggest that *Daceton armigerum* is a relatively very primitive member of the Dacetini but already well diverted from the mainstream of early tribal evolution.

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I am indebted to Mr. Harry Beatty, Dr. P. H. van Doesburg, and Dr. D. C. Geijskes for their invaluable aid in locating the Surinam colony. In fact, it was Mr. Beatty, a professional collector for the Chicago Natural History Museum, who succeeded in discovering foraging workers after I had searched fruitlessly for the species around Paramaribo for two weeks. Dr. Geijskes' assistant, Mr. Stefanus Ligorie, gave important help in dissecting the nest. I am further grateful for the assistance of Dr. A. D. Blest, Mr. Thomas Collett, and Mr. Eric Edler in locating and studying the Trinidad colony. The field study was supported in part by a grant from the National Science Foundation.

REFERENCES CITED

Brian, M. V.
1956. Group form and causes of working inefficiency in the ant *Myrmica rubra* L. Phys. Zool., **29**:173-194.

Brown, W. L.
1949. Revision of the tribe Dacetine: IV. Some genera properly excluded from the Dacetini, with the establishment of the Basicerotini, new tribe. Trans. Amer. Ent. Soc., **75**:83-96.

Brown, W. L. and E. O. Wilson
1960. The evolution of the dacetine ants. Quart. Rev. Biol., **34**:278-294.

Crawley, W. C.
1916. Ants from British Guiana. Ann. Mag. Nat. Hist., (8)**17**:366-378.

Mann, W. M.
1916. The Stanford Expedition to Brazil, 1911, John C. Branner, Director. The ants of Brazil. Bull. Mus. Comp. Zool., **60**:399-490, 7 plates.
1922. Ants from Honduras and Guatemala. Proc. U.S. Nat. Mus., **61**: 1-54.

McCook, H.
1878. Toilet habits of ants. Proc. Acad. Nat. Sci. Philadelphia, pp. 119-122.

Weber, N. A.
1949. The functional significance of dimorphism in the African ant, *Oecophylla*. Ecology, **30**:397-400.

Wilson, E. O.
1953. The ecology of some North American dacetine ants. Ann. Ent. Soc. Amer., **46**:479-495.
1962. Chemical communication among workers of the fire ant *Solenopsis saevissima* (Fr. Smith). Animal Behaviour, **10**:134-164.

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THE GENUS *TETRAGNATHA* (ARANEAE, ARGIOPIDAE) IN JAMAICA, W. I.

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CAMBRIDGE, MASS., U.S.A.
PRINTED FOR THE MUSEUM
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No. 8 — *The Genus Tetragnatha (Araneae, Argiopidae) in Jamaica, W. I.*

By Arthur M. Chickering
Albion College, Albion, Michigan

During my visit to Jamaica, W. I. in the fall of 1957 I made an effort to collect as many specimens of the genus *Tetragnatha* Latreille, 1884 as possible. On the basis of collections previously made by myself and others I had already (1957) been able to report six species to be present in this interesting island: *T. antillana* Simon, *T. caudata* Emerton, *T. exigua* Chickering, *T. pallescens* F. P.-Cambridge, *T. tenuissima* O. P.-Cambridge, and *T. visenda* Chickering. As a result of rather painstaking search for these animals from the middle of September, 1957, until the middle of December of the same year I can now definitely add seven species to the total number formerly known to occur in Jamaica. The complete list can now be given as follows: *T. antillana* Simon, *T. caudata* Emerton, *T. elongata* Walckenaer, *T. elyunquensis* Petrunkevitch, *T. exigua* Chickering, *T. farri* sp. nov., *T. guatemalensis* O. P.-Cambridge, *T. lewisi* sp. nov., *T. orizaba* (Banks), *T. pallescens* F. P.-Cambridge, *T. subextensa* Petrunkevitch, *T. tenuissima* O. P.-Cambridge, *T. visenda* Chickering. Only females are known for *T. farri* sp. nov., *T. elyunquensis* Petrunkevitch, and *T. subextensa* Petrunkevitch. Only males are known for *T. lewisi* sp. nov. and *T. visenda* Chickering. Both sexes are known for the remaining eight species. I had expected that *T. piscatoria* Simon would be found on the island but up to the present time this species had not appeared in the collections. I have had specimens from the British Museum (Natural History) selected from the original collection and on loan for study, however. For extensive bibliographies the reader is referred to Roewer (1942) and Bonnet (1959). Only those publications considered most pertinent are cited in this paper. Helpful figures of species treated in this paper have been published by several authors. The following publications are suggested as references: F. P.-Cambridge (1903); Petrunkevitch (1930); Seeley (1928); Chickering (1957a, 1957b). In the subject matter dealing with each species treated in this paper I have tried to record the most important external features concerned with identification. Variations among the structural characteristics have been noted with respect to nearly every

species and these should be taken into consideration whenever one is making an extensive study of the genus. This has been done altogether too infrequently in past studies and has often led to errors and misconceptions. It is hoped that the drawings of various parts which accompany the descriptive material on each species will be helpful to those in Jamaica who are attempting to gain a comprehensive view of the arthropod fauna of the island. Whenever possible these drawings have been made directly from Jamaican specimens and sometimes differ somewhat from previously published drawings. This is caused by the inadequacy of some of the previously published figures, natural variations within species, and the fact that such parts as the terminations of the male palpal conductor and embolus have quite different appearances when viewed from different angles. Holotypes will be deposited in the Museum of Comparative Zoology at Harvard College.

Acknowledgments are again due and gratefully rendered to individuals and organizations as specifically mentioned in several recent publications (1957a, 1959, 1960). In addition to these I will now add the names of Mr. C. Bernard Lewis, Director, Mr. R. P. Bengry, and Dr. T. H. Farr, all of whom are on the staff of the Science Museum of the Institute of Jamaica and all of them aided me greatly in my field work during my stay of three months in Jamaica in the fall of 1957.

Keys to the Species of TETRAGNATHA *from Jamaica, W. I.*

Males

1. Lateral eyes farther from one another than AME are from PME (*caudata, lewisi, orizaba, pallescens*) 2

1a. Lateral eyes closer to one another than AME are to PME (*antillana, elongata, exigua, guatemalensis, tenuissima, visenda*) 5

2. With abdomen conspicuously extended posterior to spinnerets ..... *caudata*, p. 430

2a. With abdomen not conspicuously extended posterior to spinnerets (*lewisi, orizaba, pallescens*) 3

3. Promargin of the fang groove without the conspicuous "large tooth" ..... *pallescens*, p. 444

3a. Promargin of the fang groove with the "large tooth" standing as either the second or third from the distal end (*lewisi, orizaba*) 4

4. The conductor of the palpal tarsus an elongated, gently curved structure without any special terminal modification ..... *lewisi*, p. 439

4a. Palpal conductor modified distally into a beak-like structure ..... *orizaba*, p. 442

5. All legs devoid of spines (*exigua, tenuissima*) 6
5a. All legs with spines (*antillana, elongata, guatemalensis, visenda*) 7
6. Prolateral spur on basal segment of chelicera not bifurcated distally; a small species, not more than 3-4 mm. in length .....*exigua*, p. 435
6a. Prolateral spur on basal segment of chelicera definitely bifurcated distally; a much larger species, 8-9 mm. in length ...*tenuissima*, p. 447
7. Promargin of fang groove without the "large tooth" as usually regarded .....*antillana*, p. 428
7a. Promargin of fang groove with the "large tooth" occupying the third place from the distal end (*elongata, guatemalensis, visenda*) 8
8. Paracymbium terminating in a slender digital extension ....*guatemalensis*, p. 438
8a. Paracymbium without any slender, digital, terminal extension (*elongata, visenda*) 9
9. Palpal patella and tibia both short with tibia longer than patella in ratio of about 3 : 2..... ... *visenda*, p. 448
9a. Palpal patella and tibia elongated with tibia nearly or fully twice as long as the patella .....*elongata*, p. 431

Females

1. Lateral eyes farther from one another than AME are from PME (*caudata, orizaba, pallescens*) 2
1a. Lateral eyes closer to one another than AME are to PME (*antillana, elongata, elyunquensis, exigua, farri, guatemalensis, subextensa, tenuissima*) 4
2. Abdomen conspicuously extended posterior to spinnerets .... *caudata*, p. 430
2a. Abdomen not conspicuously extended posterior to spinnerets (*orizaba, pallescens*) 3
3. Basal segment of chelicera about half as long as carapace; genital fold several times as wide as long; retromargin of fang groove with 5-6 teeth .....*orizaba*, p. 442
3a. Basal segment of chelicera about four-fifths as long as carapace; genital groove about twice as wide as long; the retromargin of fang groove with about ten teeth ..... . *pallescens*, p. 444
4. Abdomen short, compact, about half as broad as long; lateral eyes nearly contiguous ..... . *elyunquensis*, p. 433
4a. Abdomen relatively long and slender; lateral eyes not nearly contiguous (*antillana, elongata, exigua, farri, guatemalensis, subextensa, tenuissima*) 5
5. Spines completely lacking from legs (*exigua, tenuissima*) 6
5a. Legs at least fairly well supplied with spines (*antillana, elongata, farri, guatemalensis, subextensa*) 7
6. A small species, not more than 3-4 mm. in length; only about 5-6 teeth along each margin of fang groove ..... .*exigua*, p. 435

6a. A larger species, about 10-11 mm. long; about 8-9 teeth along each margin of fang groove ..... *tenuissima*, p. 447

7. Retromargin of fang groove with a large distal tooth conspicuously extended apically (Fig. 5); genital fold considerably longer than wide at base ..... *antillana*, p. 428

7a. Retromargin of fang groove without an enlarged and extended distal tooth; genital fold not longer than wide at base (*elongata, farri, guatemalensis, subextensa*) 8

8. Fang with a conspicuous retrolateral cusp at its base (Fig. 33) ..... *farri*, p. 435

8a. Fang without any conspicuous retrolateral cusp at its base (small dorsal cusps may be present) (*elongata, guatemalensis, subextensa*) 9

9. Basal segment of chelicera with a more or less well developed dorsal cusp at distal end (Fig. 19) ..... *elongata*, p. 431

9a. Basal segment of chelicera without any dorsal cusp at distal end (*guatemalensis, subextensa*) 10

10. With a more or less conspicuous dorsal abdominal gibbosity; basal segment of chelicera about one-third as long as carapace ..... *subextensa*, p. 445

10a. Without any conspicuous dorsal abdominal gibbosity; basal segment of chelicera about half as long as carapace ..... *guatemalensis*, p. 438

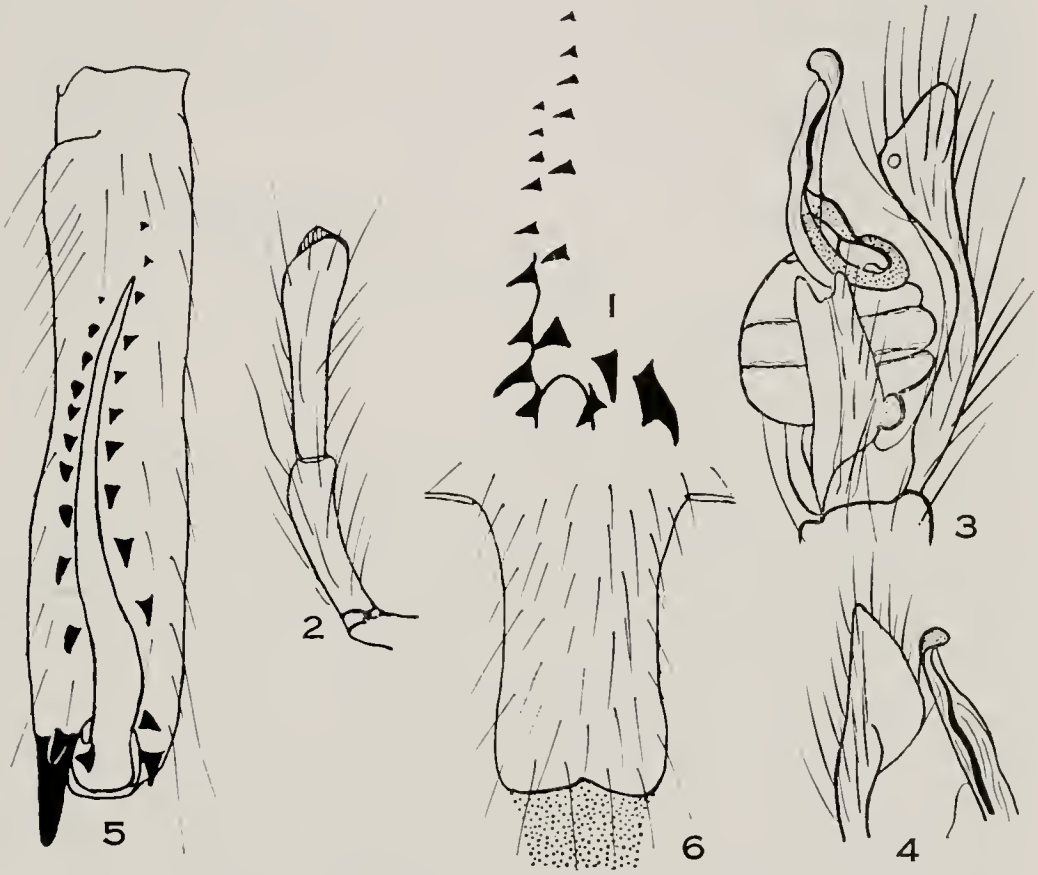
Tetragnatha antillana Simon, 1897
(Figures 1-6)

T. antillana, F. P.-Cambridge, 1903.
T. eremita Chamberlin, 1924.
T. antillana Seeley, 1928.
T. antillana, Petrunkevitch, 1930.
T. apheles Chamberlin and Ivie, 1936 (females only).
T. festina Bryant, 1945 (male only).
T. haitiensis Bryant, 1945 (females only).
T. antillana Kraus, 1955.
T. antillana Chickering, 1957a, 1957b.

This species appears to be widely distributed through Mexico, Central America, much of South America to Argentina, and also much of the West Indian region. It is one of the largest species thus far reported from the Island of Jamaica.

Males. Length about 8-9 mm. without chelicerae; including chelicerae about 10.5 to 11 mm. or even larger. Legs with numerous spines of moderate length. Lateral eyes closer to one another than AME are to PME. Chelicerae: porrect and quite divergent in distal halves; basal segment nearly as long as carapace; there is no "large tooth" on the promargin of the fang groove but the spur and two contiguous teeth form a conspicuous group of

three; the spur itself is usually robust and definitely bifurcate distally; the complete dentition is shown in Figure 1. Palp: the patella is about two-thirds as long as the tibia and both are considerably elongated (Fig. 2); the paracymbium is distally bifid; the fang is moderately sinuous and has irregularities along its inner surface; the conductor and embolus terminate as shown in Figures 3 and 4.



External Anatomy of *Tetragnatha*
Figures 1-6, *T. antillana*

FIG. 1. Cheliceral teeth of male.
FIG. 2. Palpal tibia and patella.
FIGS. 3-4. Palpal tarsus; two different views.
FIG. 5. Left chelicera of female; ventral view.
FIG. 6. Genital fold of female.

Females. Length about 9-10 mm. without chelicerae; with chelicerae 11-12 mm. Spines on legs and eyes essentially as in males. Chelicerae: moderately porrect and moderately divergent; basal segment a little more than two-thirds as long as the

carapace; there is a large and quite distinctive distal retromarginal tooth and other teeth along the fang groove as indicated in Figure 5; the fang is moderately sinuous and there is usually a small dorso-retrolateral cusp near its base. The form of the genital groove is shown in Figure 6.

Collection records. Both sexes have been collected at numerous localities during the past few years. It was found to be abundant at St. Catherine, Guanaboa Vale, November and December, 1957, and at Mavis Bank, March, 1953 (R. P. Bengry); also collected at St. Catherine, Guanaboa Vale, February, 1958 (R. P. Bengry), and November, 1958 (T. H. Farr). Also taken several times in St. Andrew and St. Thomas parishes.

Tetragnatha caudata Emerton, 1884
(Figures 7-13)

T. lacerta Petrunkevitch, 1911.
T. caudata Seeley, 1928.
T. lacerta Roewer, 1942.
T. caudata Chickering, 1957a, 1957b.

Males. Average length with chelicerae about 8 mm.; slender with abdomen conspicuously extended posterior to spinnerets thus producing what has been called a "tail"; legs are long, slender, with few weak spines. Eyes: laterals plainly farther from one another than AME are from PME. Palp: patella and tibia both relatively short with little difference in length; paracymbium bluntly rounded at distal end; the conductor is curiously dilated and minutely spined distally; variations have been noted in respect to this terminal dilation in specimens from different localities and it is suggested these differences may be due in part to distortion in the preservative (Figs. 8-9). Chelicerae: the fang is regularly curved without being sinuate; the basal segment is about two-thirds as long as the carapace; the promarginal "large tooth" is conspicuous and there are about seven other teeth on this margin; the retromargin of the fang groove has a series of about 8-9 teeth (Fig. 7).

Females. Average length with chelicerae about 9-10 mm. Abdomen even more conspicuously extended posterior to spinnerets than in males; notched at its base; the degree of extension posterior to spinnerets differs in different specimens in preservation because of the ability of each individual to extend or retract this part of its body in the living state. Chelicerae: basal segment about half as long as carapace; promargin of fang groove with

about 6-7 teeth, retromargin with about the same number; the base of the fang usually has a dorsal cusp. The genital groove and area are about half as long as wide at base (Fig. 13).

Collection records. The species appears to be rare in Jamaica as in many other regions where it has been reported. I have but one record from this island: Papine, April, 1937, five miles north of the city of Kingston. The species did not appear in my collections of 1957.

External Anatomy of *Tetragnatha*
Figures 7-13, *T. caudata*

FIG. 7. Left cheliceral dentition of male.

FIG. 8. Palpal patella, tibia, and tarsus of male; one view of distal end of conductor.

FIG. 9. Another view of tip of cymbium and distal end of conductor.

FIG. 10. Left lateral view of abdomen of female.

FIG. 11. Left cheliceral dentition of female.

FIG. 12. Eye group of female from in front.

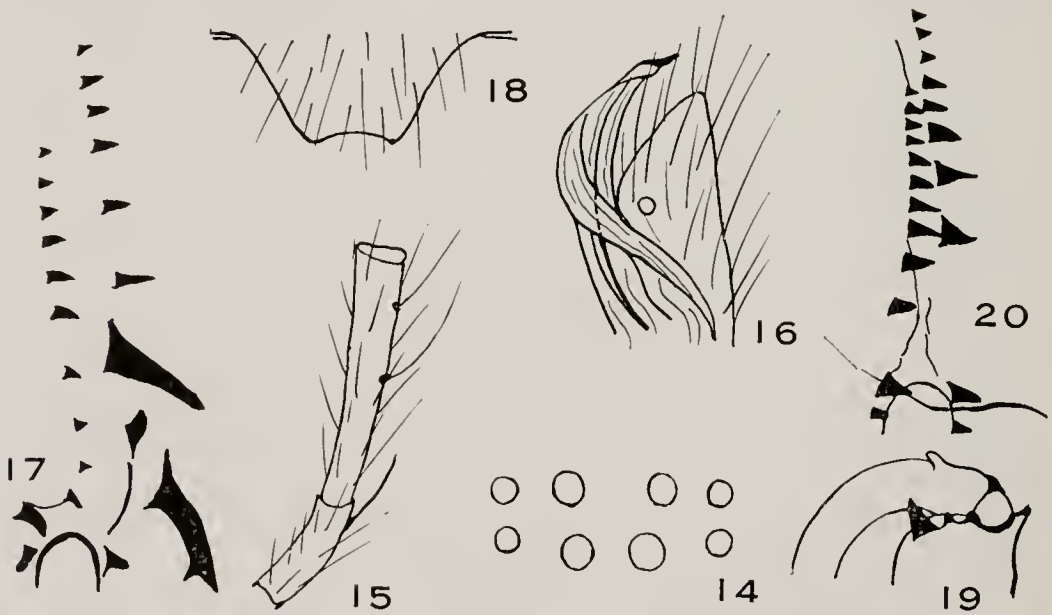
FIG. 13. Genital fold of female.

TETRAGNATHA ELONGATA Walckenaer, 1805
(Figures 14-20)

T. grallator Keyserling, 1865.
T. elongata Seeley, 1928.
T. elongata Bryant, 1940.
T. elongata Bryant, 1945.
T. elongata Chickering, 1959.

This species is known to be widely distributed throughout the United States, from Mexico to the Arctic regions, and has been reported from Cuba, Hispaniola, and Colombia. It has not yet appeared in my Panamanian collections and I am doubtful about the accuracy of the South American identifications. I can now definitely report it from Jamaica, W. I.

Males. Average length including chelicerae about 9-10 mm. Abdomen not extended posterior to spinnerets and not gibbous at base. Lateral eyes closer to one another than AME are to PME (Fig. 14). Spines on legs fairly long and moderately robust. Palp: tibia nearly twice as long as patella and both are considerably elongated (Fig. 15); paracymbium bluntly rounded distally; conductor curved and sharply pointed at tip (Fig. 16). Chelicerae: basal segment usually as long as the carapace; the spur is plainly bifurcate distally; the "large tooth" is conspicuous on the promargin of the fang groove together with seven



External Anatomy of *Tetragnatha*
Figures 14-20, *T. elongata*

Fig. 14. Eye group of male, from in front.

Fig. 15. Palpal patella and tibia of male.

Fig. 16. Tips of cymbium, embolus, and conductor.

Fig. 17. Left cheliceral teeth of male.

Fig. 18. Genital groove of female.

Fig. 19. Distal end of basal segment of chelicera, base of fang and associated structures.

Fig. 20. Left cheliceral teeth of female.

or eight smaller teeth; the retromargin has a series of from 10 to 13 teeth most of which are relatively small (Fig. 17); the fang is somewhat sinuate.

Females. Average length with chelicerae about 13 mm. Abdomen: not continued posterior to spinnerets; considerably swollen at base which is only slightly concave; genital fold and area much wider at base than long (Fig. 18). Eyes essentially as in male. Spines essentially as in male also. Chelicerae: basal segment nearly as long as carapace and typically with a small dorsal distal tooth (Fig. 19); the fang is moderately sinuous and has a basal dorsal cusp; the promargin of the fang groove has about 8-11 teeth with a considerable space between the second and third; the retromargin has about 12-13 teeth with a shorter space between the second and third.

Collection records. St. Thomas, Roselle Falls, October 29th, 1957; St. Catherine, near Bushey Park, December 2, 1957; St. Andrew, Hermitage Reservoir, November 26th, 1957; St. Andrew, Ferry, November 27, 1958 (T. H. Farr).

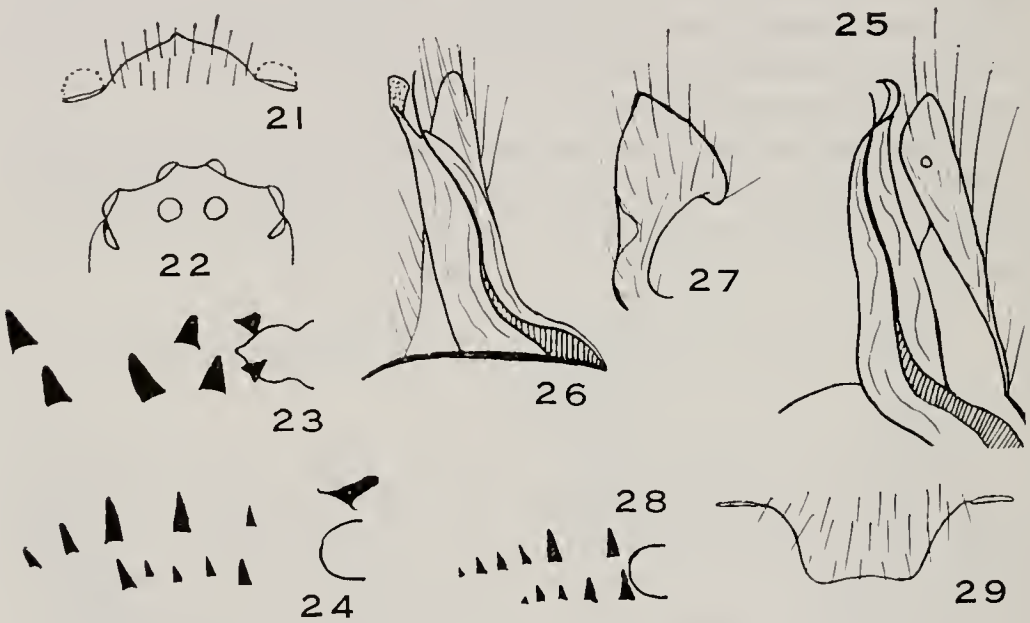
Tetragnatha elyunquensis Petrunkevitch, 1930
(Figures 21-23)

The females of this species were described from Porto Rico where they were found at the summit of El Yunque in October, 1925. The males are still unknown. It was pointed out by Dr. Petrunkevitch that the generic relationships of this species are not clear. He suggested that it might be more closely related to *Pachygnatha* and even had some features which suggested *Meta*. It will be interesting to see the male when it is found.

Females. Total length with chelicerae about 5-6 mm. Abdomen: the shape varies considerably and in some of the older specimens becomes very gibbous in the middle of the dorsal region; usually more than half as broad as long; not notched or concave at base; in general, relatively short and compact; not continued posterior to spinnerets; genital groove and area very gently extended so that the groove itself would be said to be gently procurved and not angular (Fig. 21). Eyes: with LE very close together and medians well separated; central ocular quadrangle only slightly wider behind than in front (Fig. 22). Spines on legs rather short and fairly robust. Palpal claws without discernible teeth. Chelicerae: short, robust; slightly more than half as long as carapace; fang evenly curved; fang groove with three promarginal teeth, the second very small, close to the first and far

separated from the third; on the retromargin there is a relatively large, blunt, somewhat irregular tooth at the base of the fang (not represented in Petrunkevitch's original drawing), two more close together, a short space and then two more (some variations have been noted among the specimens available for study) (Fig. 23).

Collection records. The species has been taken at the following localities: St. Andrew, Hermitage Reservoir, October 30, November 5, 1957; Portland, Hardwar Gap, November 20, 1957 and Deeember 8, 1958 (T. H. Farr).



External Anatomy of *Tetragnatha*
Figures 21-23, *T. elyunquensis*
Figures 24-29, *T. exigua*

Fig. 21. Genital groove of female.
Fig. 22. Eye group of female, from above.
Fig. 23. Left cheliceral teeth of female.
Fig. 24. Left cheliceral teeth of male.
Fig. 25. Distal ends of cymbium, conductor, and embolus.
Fig. 26. *Idem*, from a different view.
Fig. 27. Paracymbium of male.
Fig. 28. Left cheliceral teeth of female.
Fig. 29. Genital groove of female.

Tetragnatha exigua Chickering, 1957
(Figures 24-29)

Males. Total length with chelicerae a little less than 3 mm. Abdomen slender; not extended posterior to spinnerets. Eyes with laterals somewhat closer to one another than AME are to PME. Chelicerae: moderately porrect; quite divergent in distal two-thirds; prolateral spur simple, not bifurcate distally; fang slender, slightly sinuate, with a blunt tubercle on its inner margin about one-fifth of its length from the base; basal segment about half as long as the carapace; the "large tooth" is absent from the promargin of the fang groove but there are five teeth on this margin and about five on the retromargin (Fig. 24); variations in the dentition have been noted. Spines are completely lacking from the legs just as in *T. tenuissima.* Palp: both tibia and patella are short with the tibia somewhat the longer; the paracymbium (Fig. 27) is unusually broad; the conductor appears to terminate in a sharp, fine, claw-like point (Figs. 25-26).

Females. Total length with chelicerae about 3-4 mm. Abdomen: slender and not extended posterior to spinnerets; the genital groove and area are about half as long as wide at base (Fig. 29). Eyes: essentially as in male; an erroneous statement regarding position of the eyes occurs in the original description. All spines lacking from the legs as in male. Chelicerae: moderately well developed; fairly robust; nearly vertical and parallel; basal segment about one-third as long as carapace; fang slender and evenly curved; promargin of fang groove with about four moderately well developed teeth and retromargin with about four or five smaller teeth (frequent variations have been noted).

Collection records. The original specimens were from Hanover, Askenish, Trail to Dolphin Head, June 24, 1954. Since that time the species has been taken at Portland, Hardwar Gap, October 2, and November 20, 1957.

Tetragnatha farri sp. nov.
(Figures 30-33)

A few years ago while studying this genus as it was understood in Jamaica, W. I., at that time (1957), I stated that I considered two females from St. Croix, Virgin Islands, erroneously filed as *T. antillana* Simon to belong to *T. confraterna* Banks. In the light of my continued study of the genus and the species

here described together with a re-examination of the two specimens from St. Croix I am now of the opinion that they all belong to a new species which I am naming in honor of Dr. T. H. Farr with whom I collected extensively during my visit to Jamaica in the fall and early winter of 1957. For these reasons I am compelled to conclude that *T. confraterna* Banks has not yet been positively identified from the West Indies. It is my opinion, however, that *T. farri* sp. nov. is closely related to *T. confraterna* Banks but the characteristics of the genital groove, chelicceral teeth, and perhaps other features serve to separate them quite definitely.

Female holotype. Total length with chelicerae 10.205 mm., without the chelicerae 8.45 mm. Carapace 2.795 mm. long, 1.69 mm. wide opposite second coxae where it is widest; with the usual form of the genus; median fovea broad and subdivided into two shallow depressions.

Eyes. Eight in two rows as usual; ocular tubercles moderately developed; viewed from above, both rows moderately recurved; viewed from in front, anterior row almost straight, posterior row slightly procurved, all measured by centers. Central ocular quadrangle wider behind than in front in ratio of 17 : 14, only slightly wider behind than long. Ratio of eyes AME : ALE : PME : PLE = 10 : 6 : 8 : 8. AME separated from one another by about 1.1 times their diameter, from ALE by 1.8 times their diameter. PME separated from one another by slightly more than twice their diameter, from PLE by 2.5 times their diameter. Laterals separated from one another by about 11/8 of their diameter. AME separated from PME by about 1.4 times the diameter of AME and, therefore, slightly farther from one another than ALE are from PLE. Height of clypeus equal to nearly 1.5 times the diameter of AME. (In a paratype the lateral eyes appear to be slightly farther from one another than AME are from PME.)

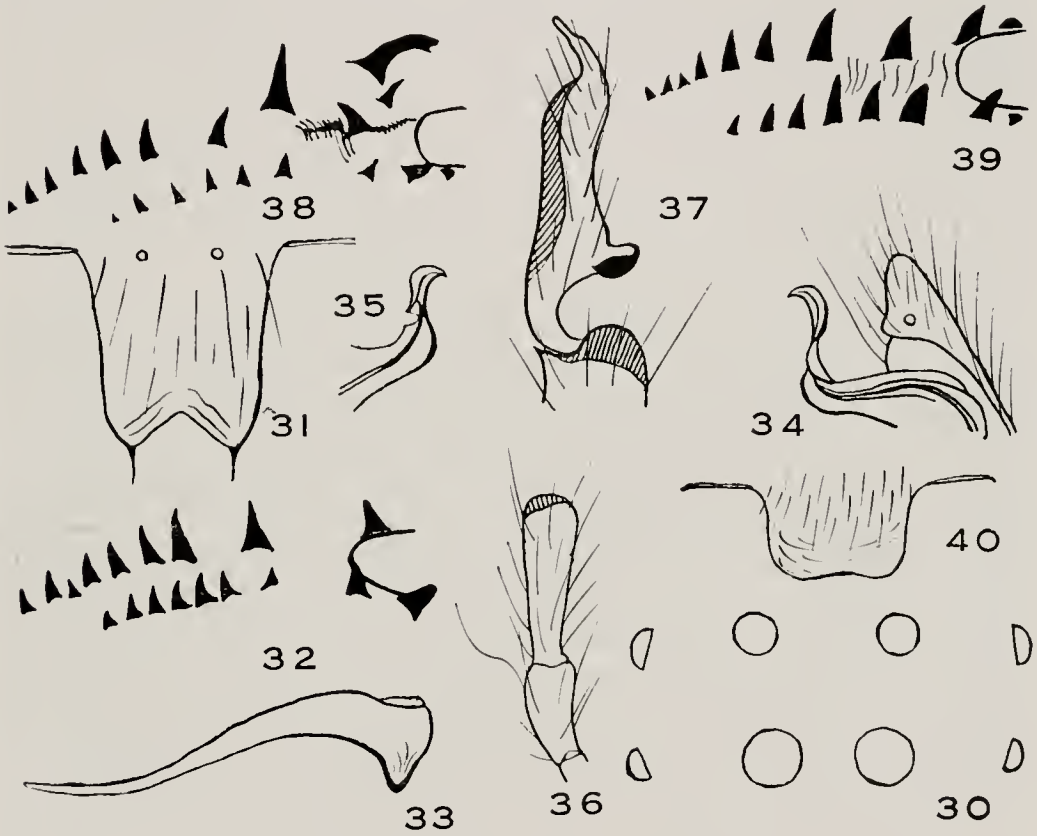
Chelicerae. Moderately porrect and quite divergent; basal segment 2.00 mm. long and, therefore, about three-fourths as long as carapace. Fang quite sinuous, with a conspicuous retrolateral cusp near its base (Fig. 33) and an elevation near the middle of its inner surface. Promargin of fang groove with nine teeth (some irregularity noted between right and left sides); retromargin with nine teeth (Fig. 32).

Maxillae. Quite typical of the genus; slightly divergent and somewhat broadened distally; somewhat more than three times

as long as wide in middle; a little more than twice as long as lip.

Lip. Slightly wider at base than long; sternal suture only very slightly procurved; with pronounced sternal tubercles at ends of suture.

Sternum. Generally scutiform; moderately convex; moderately scalloped opposite each coxa and produced between all coxae; continued as a narrow sclerite between fourth coxae which are separated by about one-third of their width.



External Anatomy of *Tetragnatha*
Figures 30-33, *T. farri*
Figures 34-40, *T. guatemalensis*

Fig. 30. Eye group of female.
Fig. 31. Genital groove of female.
Fig. 32. Cheliceral teeth of female.
Fig. 33. Left fang of female showing basal cusp.
Fig. 34. Distal ends of cymbium, conductor, and embolus.
Fig. 35. Another view of distal ends of conductor and embolus.
Fig. 36. Palpal patella and tibia of male.
Fig. 37. Paracymbium of male.
Fig. 38. Left cheliceral teeth of male.
Fig. 39. Left cheliceral teeth of female.
Fig. 40. Genital groove of female.

Legs. 1243. Width of first patella at "knee" .330 mm., tibial index of first leg 6. Width of fourth patella at "knee" .286 mm., tibial index of fourth leg 8.

	Femora	Patellae	Tibiae	Metatarsi	Tarsi	Totals
	(All measurements in millimeters)					
1.	4.940	1.060	4.550	5.005	1.430	16.985
2.	3.835	.890	3.250	3.250	.910	12.135
3.	1.950	.520	1.235	1.365	.650	5.720
4.	3.770	.650	2.860	2.925	.845	11.050

All legs with spines and hair. Spines of moderate size. All femora with trichobothria. Palpal claw with a series of fine teeth.

Abdomen. Considerably swollen in anterior half; unnotched at base; 6.5 mm. long including spinnerets; not extended posterior to spinnerets; genital fold deeply notched at posterior border, about as wide at base as long (Fig. 31).

Color in alcohol. Color pattern well marked. Legs: in general yellowish but with many grayish streaks and spots; several segments terminate in reddish brown rings. Carapace: with a broad central gray stripe, widened in cephalic region; with a gray marginal stripe on each side. Chelicerae with varying shades of gray; fang deep reddish brown. Sternum and lip brownish gray. Maxillae nearly white in median half and gray in lateral half. Abdomen: dorsum and lateral sides with many nearly black spots and streaks with silvery spots and streaks; venter with a median brownish gray stripe on each side of which is a light stripe composed of a large number of silvery flecks. Color pattern difficult to describe adequately and probably quite variable in the species.

Type locality. Female holotype from St. Catherine, three miles east of May Pen, November 22, 1957. There is one paratype from St. Andrew, Hermitage Reservoir, November 26, 1957.

Tetragnatha guatemalensis O. P.-Cambridge, 1889.

(Figures 34-40)

T. guatemalensis F. P.-Cambridge, 1903.

T. seneca Seeley, 1928.

T. banksi Levi and Field, 1954.

T. guatemalensis Chickering, 1957a, 1957b.

Males. Total length with chelicerae about 7-8 mm. (somewhat smaller than those from Panama). Abdomen not extended posterior to spinnerets. Eyes: lateral eyes closer to one another

than AME are to PME. Spines are present on the legs in moderate numbers and size. Palp: tibia longer than patella in ratio of about 3 : 2; both of moderate length; paracymbium terminates in a slender digital process, quite distinctive; conductor and embolus terminate in distinctive manner (Figs. 34-37). Chelicerae: the fang has a small basal dorsal cusp and has a low elevation on its inner margin near the middle; the spur is indistinctly bifid; the promargin of the fang groove has the "large tooth" moderately well developed together with eight other teeth placed in positions typical of the Panamanian members of the species; the retromargin has nine teeth also placed essentially as they are on those from Panama; the northern members of the species seem to alter the arrangement and relative sizes of the teeth to some extent; the basal segment of the chelicera is very divergent in its distal two-thirds and is about four-fifths as long as the carapace.

Females. Total length with chelicerae about 9-10 mm. in fully matured individuals. Abdomen: not continued posterior to spinnerets; considerably swollen in anterior half; genital groove (Fig. 40) a little less than half as long as wide at base. Eyes essentially as in male. Spines on legs numerous and rather short. Palpal claw finely serrated. Chelicerae: basal segment only a little more than half as long as carapace; promargin of fang groove with about ten teeth, the last two or three of which are very small (Fig. 39); the retromargin has about eight teeth.

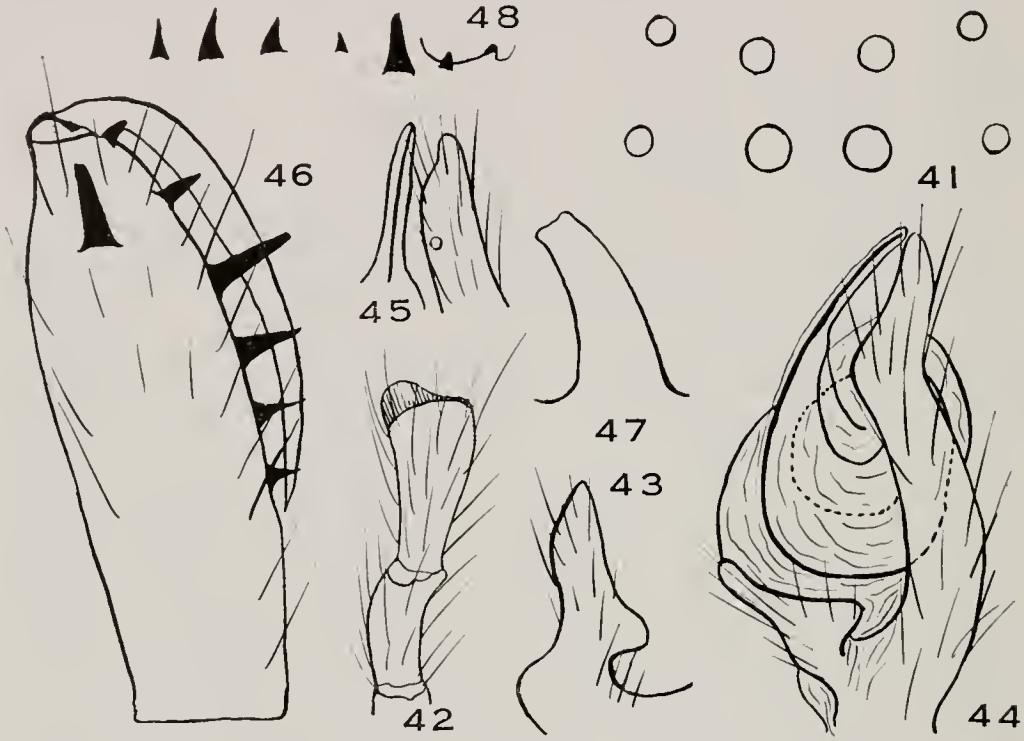
Collection records. St. Catherine, Old Harbour, October 9 and December 7, 1957; St. Catherine, Rio Cobre Gorge, November 7, 1957; St. Catherine, Guanaboa Vale, November, 1958; St. Catherine, near Bushey Park, December 2, 1957; St. Andrew, Richards Reservoir, December 3, 1957.

Tetragnatha lewisi sp. nov.

(Figures 41-48)

The male described below as the holotype of a new species is considerably damaged with its abdomen detached and legs mutilated. For a time it was thought best not to describe it until better specimens are available. However, because the species represented by this specimen has certain unusual features it was finally decided to describe it even though it is damaged to some extent. This decision was based in part upon advice of colleagues in the Museum of Comparative Zoology at Harvard College.

Holotype male. Total length including chelicerae about 7.8 mm. Carapace 2.145 mm. long, 1.32 mm. wide opposite second coxae where it is widest; with the usual form of the genus; median fovea divided into two shallow depressions.



External Anatomy of *Tetragnatha*
Figures 41-48, *T. lewisi*

Fig. 41. Eye group of male from in front.
Fig. 42. Palpal patella and tibia of male.
Fig. 43. Paracymbium of male.
Fig. 44. Palpal tarsus of male.
Fig. 45. Another view of distal end of cymbium, conductor, and embolus of male.
Fig. 46. Left chelicera of male showing spur and teeth along the promargin of fang groove.
Fig. 47. Spur from chelicera, much enlarged, showing bevelled distal end.
Fig. 48. Teeth along the retromargin of the fang groove.

Eyes. Eight in two rows as usual; ocular tubercles bearing ALE are most pronounced. Viewed from above, both rows recurved; viewed from in front, posterior row somewhat recurved, anterior row almost straight, all measured by centers. Central ocular quadrangle wider behind than in front in ratio of

about 7 : 6, about as long as wide behind. Ratio of eyes AME : ALE : PME : PLE = 9 : 5 : 6 : 5. AME separated from one another by about eleven-ninths of their diameter, from ALE by twice their diameter. PME separated from one another by about 2.5 times their diameter, from PLE by a little more than twice their diameter. Laterals separated from one another by nearly 3.5 times their diameter. AME separated from PME by about twice the diameter of PME and, therefore, closer to one another than ALE are to PLE (Fig. 41). Height of clypeus equal to about 1.5 times the diameter of AME.

Chelicerae. Only slightly porrect; slightly divergent in distal half; basal segment about 1.3 mm. long and, therefore, about two-thirds as long as the carapace; fang only slightly sinuous; the prolateral spur is not distally bifid but it is slightly bevelled there. The promargin of the fang groove apparently has six teeth of which the third from the base of the fang is the so-called "large tooth" but it is not strongly developed; the retromargin also has six teeth of which the second from the base of the fang is the largest (Figs. 46-48). Note: figures of teeth reconstructed by use of both right and left chelicerae because of injury to certain teeth.

Maxillae. Nearly parallel; slightly widened and divergent at distal ends; three times as long as wide in middle; longer than lip in ratio of about 3 : 1.

Lip. Broader at base than long in ratio of about 17 : 12; sternal suture gently procurved; lateral sternal tubercles well developed.

Sternum. Elongate scutiform; longer than wide between second coxae in ratio of about 3 : 2; extended between coxae as narrow selerites; fourth coxae separated by about two-thirds of their width.

Legs. 1243 (estimated from incomplete data because of mutilation). Width of first patella at "knee" .242 mm., tibial index of first leg 4. Width of fourth patella at "knee" .190 mm., tibial index of fourth leg 5.

	Femora	Patellae	Tibiae	Metatarsi	Tarsi	Totals
	(All measurements in millimeters)					
1.	5.330	.845	5.330 ?	?	?	?
2.	4.130?	.650	3.315	3.575	?	?
3.	1.885	.455	1.322	1.365	.585	5.612
4.	3.900	.550	3.120	3.200	.780	11.550
Palp	1.170	.264	.308	——	1.012	2.754

Spines on legs fairly numerous and of moderate size.

Palp. Both patella and tibia short with latter only slightly longer than the former; the paracymbium (Fig. 43) has an unusual form and is considerably twisted in its course; the bulb is considerably inflated; the conductor and embolus are both very simple and follow a different course than is the case in most species (Figs. 44-45).

Abdomen. Slender; essentially cylindrical; slightly but probably not significantly extended posterior to spinnerets; unnotched at base; nearly five times as long as broad near anterior end.

Color in alcohol. Legs light yellowish with some variations. Chelicerae the same with grayish spots on prolateral surfaces. Carapace yellowish with a grayish stripe extending through the middle from PLE to posterior border. Sternum yellowish with broad, irregular, grayish margins. Abdomen: yellowish with many silvery and light golden flecks on dorsal and lateral sides; venter with a broad, median, brownish stripe and a narrow, brownish stripe in each ventrolateral position.

Type locality. Holotype male is from St. Ann, one mile east of Moneague, on Gayle Road, November 7, 1957. No paratypes and no females have yet appeared in the collections.

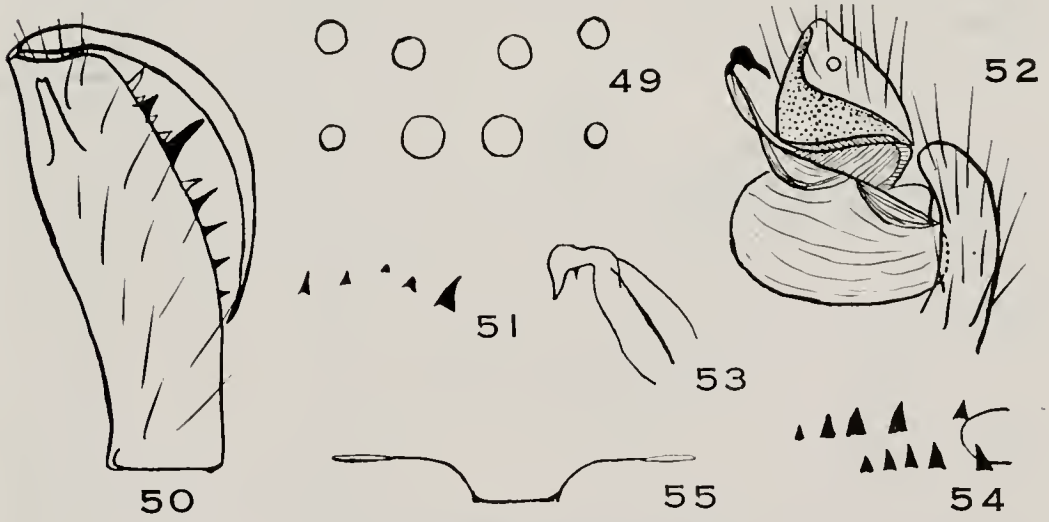
Tetragnatha orizaba (Banks), 1898
(Figures 49-55)

Eugnatha orizaba Banks, 1898.

Males. About 5-6 mm. long with chelicerae. Lateral eyes farther from one another than AME are from PME. Chelicerae: moderately well developed; moderately porrect; quite divergent in distal halves; spur moderately bifurcate distally; fang slender, slightly sinuous; promargin of fang groove with six teeth, retromargin with five and with the middle one hardly more than a small tubercle; the second promarginal tooth may be regarded as the "large tooth" so commonly figured and emphasized in descriptions; basal segment a little more than one-half as long as the carapace. Leg spines are fairly numerous and of moderate sizes. Palp: both patella and tibia short with tibia longer than patella in ratio of about 4 : 3; the paracymbium is long and slender; the conductor and embolus are shaped as shown in Figures 52-53. Abdomen: slender; only slightly concave at base; not noticeably continued posterior to spinnerets.

Females. Total length with chelicerae about 5-6 mm. Eyes essentially as in males. Chelicerae: moderately robust and fairly well developed; nearly perpendicular; somewhat divergent; basal segment a little less than half as long as carapace; fang groove with five teeth along the promargin, the last of which is very small, and also with five along the retromargin. The leg spines are few and slender. Abdomen: essentially as in male but somewhat more robust; slightly notched at base; genital groove as shown in Figure 55. Color: the carapace has a narrow light-colored border and red streaks nearly throughout its surface; the abdomen has many spangles with a pinkish tint along the dorsolateral and lateral surfaces; there is much variation in the degree of red which appears in the coloration of different individuals.

Collection records. St. Andrew, Liguanea, October 5, 1957; St. Andrew, Long Mt., October 26, 1957; St. Andrew, Red Hills Road, October 28, 1957; St. Andrew, Richards Reservoir, November 27, 1957; St. Catherine, three miles east of Old Harbour, October 21, 1957; St. Catherine, one mile west of Spanishtown, October 21, 1957; St. James, near Reading, June 23, 1954.



External Anatomy of *Tetragnatha*
Figures 49-55, *T. orizaba*

FIG. 49. Eye group of male.

FIG. 50. Left chelicera of male from in front.

FIG. 51. *Idem;* showing teeth along the retromargin of fang groove.

FIG. 52. Distal end of palpal tarsus of male.

FIG. 53. Distal end of palpal conductor and embolus; a different view and somewhat more enlarged.

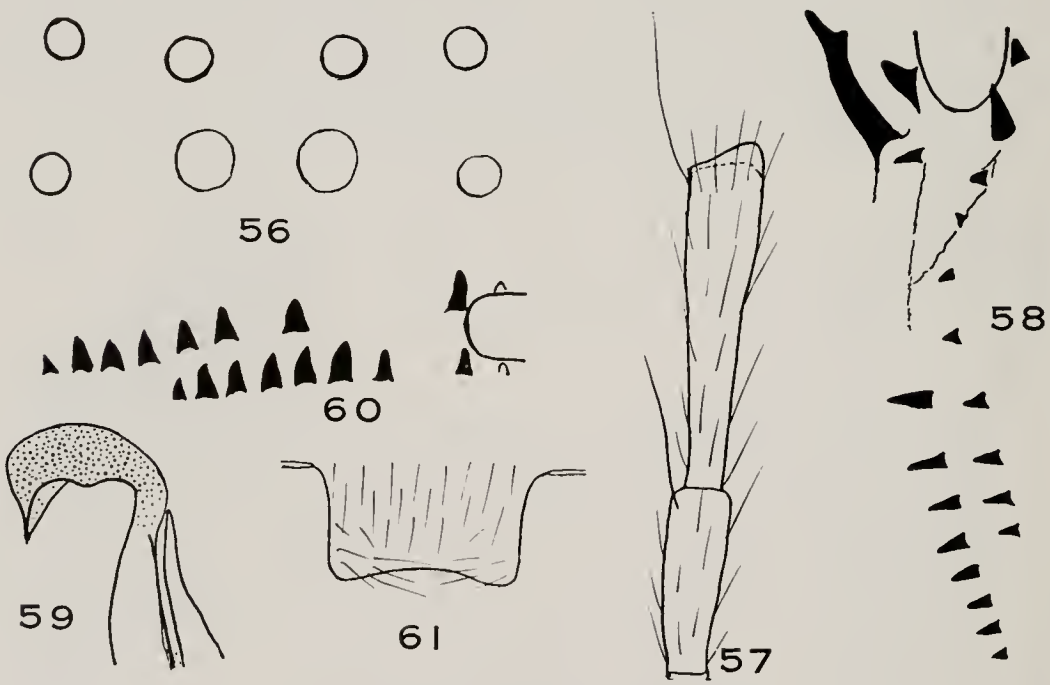
FIG. 54. Left cheliceral teeth in female.

FIG. 55. Genital groove of female.

Tetragnatha pallescens F. P.-Cambridge, 1903
(Figures 56-61)

T. pallida Banks, 1892.
Eugnatha pallida Banks, 1898.
T. pallescens F. P.-Cambridge, 1903.
T. bidens F. P.-Cambridge, 1903.
T. pallescens Seeley, 1928.
T. pallescens Petrunkevitch, 1930.
T. pallescens Bryant, 1940.
T. pallescens Bryant, 1945.
T. pallescens Chickering, 1957a, 1957b.

Males. Total length including chelicerae about 10-11 mm. Abdomen: not continued posterior to spinnerets; base of abdomen notched. Eyes: lateral eyes farther from one another than AME are from PME (Fig. 56). Spines on legs are fairly numerous and fairly conspicuous. Palp: both tibia and patella are



External Anatomy of *Tetragnatha*
Figures 56-61, *T. pallescens*

Fig. 56. Eye group of male.
Fig. 57. Palpal patella and tibia of male.
Fig. 58. Left cheliceral teeth of male.
Fig. 59. Distal end of left palpal conductor of male.
Fig. 60. Left cheliceral teeth of female.
Fig. 61. Genital grove of female.

somewhat elongated with the patella about two-thirds as long as the tibia (Fig. 57); paracymbium rather long and slender; the conductor terminates in a characteristic manner (Fig. 59). Chelicerae: the fang is only slightly sinuous; basal segment as long as the carapace; sometimes slightly longer; promarginal spur is bifurcate but the lower half of the fork is hardly more than a tubercle; the "large tooth" is absent from the promargin of the fang groove but there are about ten small teeth with a long toothless space between the second and third teeth; the retromargin of the fang groove has about ten teeth (Fig. 58).

Females. Total length with chelicerae about 10-12 mm. Abdomen not extended posterior to spinnerets; usually notched at its base; the genital groove and area nearly two-thirds as long as wide at base between openings of the book-lungs. Eyes and spines on legs essentially as in males. Palpal claw finely denticulate. Chelicerae: basal segment nearly four-fifths as long as carapace; fang moderately sinuous; promargin of fang groove with about nine teeth, the first of which is hardly more than a tubercle and with a long toothless space between the second and third; the retromargin of the fang groove has about ten teeth, the first of which is also very small; a considerable degree of variation in the dentition has been noted and in the specimen used for the figures only nine teeth were seen on each margin of the fang groove.

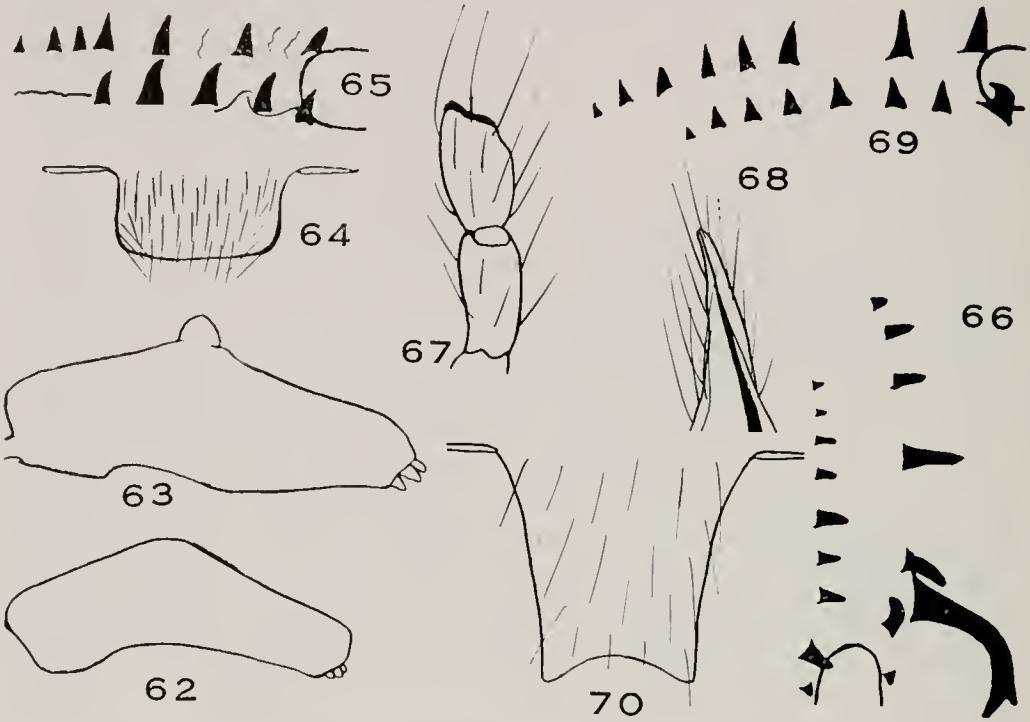
Collection records. This species is the most numerous in my collection of all the recorded species from Jamaica, W. I. It has been collected in many localities in the following parishes: St. Ann, St. Catherine, Kingston, St. Thomas.

Tetragnatha subextensa Petrunkevitch, 1930
(Figures 62-65)

T. subextensa Roewer, 1942.
T. subextensa Bonnet, 1957.

This species was described from Porto Rico and, so far as I know, has not been reported since that time; only females are known. I apparently have numerous specimens of this species from Jamaica from which the following facts are taken: total length with chelicerae about 7-9 mm. Abdomen with a pronounced dorsal hump in the middle but this gibbosity appears to be highly variable among the specimens in my collection; in some, perhaps the typical forms, it appears as shown in Figure 62; on the other hand, it sometimes appears as shown in Figure

63 where the hump is like a tubercle more or less divided along the middorsal line; not prolonged posterior to the spinnerets; genital fold about one-half as long as wide between the openings into the book-lungs (Fig. 64). Eyes: laterals closer to one



External Anatomy of *Tetragnatha*
Figures 62-65, *T. subextensa*
Figures 66-70, *T. tenuissima*

Figs. 62-63. Lateral views of abdomen of females to show differences in the gibbosity in different specimens.

Fig. 64. Genital grove of female.

Fig. 65. Left cheliceral teeth of female.

Fig. 66. Left cheliceral teeth of male.

Fig. 67. Palpal patella and tibia of male.

Fig. 68. Tip of cymbium and embolus in male.

Fig. 69. Left cheliceral teeth of female.

Fig. 70. Genital groove of female.

another than AME are to PME. Chelicerae: moderately porrect; slightly divergent; robust; somewhat convex in front; basal segment about one-half as long as carapace; promargin of fang groove usually with seven teeth and retromargin with six (as usual, variations in the dentition have been noted among specimens available for study); the fang is gently and regularly curved

and has a small dorsal cusp at its base. Numerous spines of moderate length and size occur on the legs. Color: quite variable as usual in the genus; all specimens seem to have an irregular, yellowish white (sometimes intermixed with narrow reddish streaks) band all around the margin of the thoracic part of the carapace; the "three pairs of small, black dorsal spots on abdomen" mentioned by the author of the species often appear to be obscure or lacking altogether.

Collection records. Appeared to be common in Kingston Parish, Palisadoes Area, October and November, 1957; St. Catherine, Port Henderson, October, 1957 and November, 1958; St. Andrew, Mona Road, October, 1957; Kingston, in a garden, June, 1954; St. Andrew, Richards Reservoir, November, 1957. One specimen from the Blue Mountains, S. W. side of Main Range, is tentatively assigned to this species but it is larger than other specimens and has a somewhat different tooth formula than do those assigned to the species with certainty.

Tetragnatha tenuissima O. P.-Cambridge, 1889
(Figures 66-70)

T. tenuissima F. P.-Cambridge, 1903.
T. tenuissima Petrunkevitch, 1930.
T. tenuissima Bryant, 1940.
T. tenuissima Bryant, 1945.
T. tenuissima Chickering, 1957a, 1957b.

Males. Total length with chelicerae about 8-9 mm.; very slender; abdomen not extended posterior to spinnerets. Spines are completely lacking from the legs. Lateral eyes closer to one another than AME are to PME. Legs long and slender. Palp: tibia and patella both short with tibia slightly shorter than the patella; paracymbium with chitinous nodule much more distal in position than usual; conductor terminates in a nearly straight filament (Figs. 67-68). Chelicerae: very porrect and divergent; basal segment nearly as long as carapace; fang somewhat sinuate; the prolateral spur is plainly bifurcate with the lower fork considerably longer than the upper; the "large tooth" on the promargin of the fang groove is conspicuous together with three other teeth grouped near the spur and three more posterior to the "large tooth"; the retromargin of the fang groove has about 9-10 teeth, the second and third of which are the largest (Fig. 66).

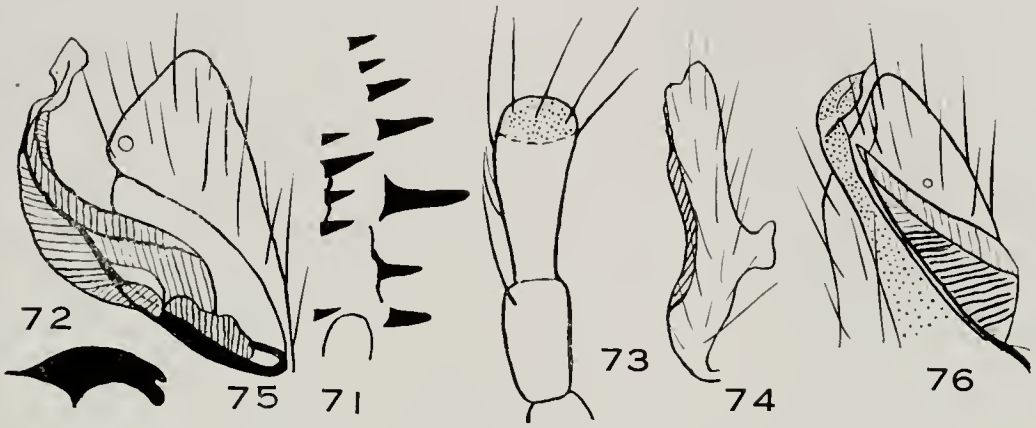
Females. Total length with chelicerae about 10-11 mm. Also slender but with abdomen somewhat swollen near base and not continued posterior to spinnerets. Eyes essentially as in male. Spines also completely lacking from legs. Genital groove and area considerably elongated (Fig. 70); fully as long as wide at base, perhaps slightly longer. Chelicerae: fang quite sinuous; the expected dorsal basal cusp seems to be lacking in all Jamaican specimens as it was in the Porto Rican specimens studied by Petrunkevitch (1930); very porrect; quite divergent; fang with a deep depression in the inner margin near the middle; basal segment about three-fourths as long as carapace; promargin of fang groove with about seven teeth and a long toothless space between second and third, retromargin with about ten teeth.

Collection records. St. Elizabeth, Maggotty, May 21, 1953 (G. R. Proctor); St. Andrew, Hermitage Reservoir, May 31, 1954 (R. P. Bengry), October 30 and November 5, 1957; St. Andrew, Mt. James, Plaintain River, October 24, 1957; St. Thomas, 6-7 miles northeast of Bath, December 10, 1957.

Tetragnatha visenda Chickering, 1957
(Figures 71-76)

Males. Total length of holotype was 8.58 mm. including chelicerae; specimens now in my collection vary in length from 5.25 mm. to that of the holotype; in general quite slender. Eyes: laterals closer to one another than AME are to PME but the degree of separation varies somewhat in different specimens. Chelicerae: somewhat porrect and divergent; basal segment slightly more than half as long as carapace; fang moderately robust, evenly curved, and with a small basal cusp on the dorsal side; the promargin of the fang groove with the "large tooth" well developed together with from six to eight others; the retromargin has from about five to eight in different specimens; the prolateral spur is well developed, definitely bifurcate with the larger fork directed inwardly (Figs. 71-72). The holotype has nine promarginal teeth along the fang groove and eight along the retromargin but a considerable degree of variation has been noted in respect to these structures among the specimens now available. All legs bear spines of moderate length and size. Palp: tibia and patella both short with the former longer than the latter in ratio of about 3 : 2 (Fig. 73); the paracymbium is long, slender, and notched at its distal end (Fig. 74); the conductor has a termination which appears very different when viewed from different angles (Figs. 75-76).

Collection records. St. Catherine, Port Henderson, June, 1954 and November 16, 1958 (T. H. Farr); St. Andrew, August, 1954 (G. H. Proctor); Kingston, Mona Road, October 19, 1957; Kingston, Palisadoes area, October and November, 1957 (several times).



External Anatomy of *Tetragnatha*
Figures 71-76, *T. visenda*

FIG. 71. Cheliceral teeth of male.
FIG. 72. Cheliceral spur of male.
FIG. 73. Palpal patella and tibia of male.
FIG. 74. Paracymbium of male.
FIGS. 75-76. Two different views of tip of left cymbium of male with shape of conductor emphasized.

BIBLIOGRAPHY

1959. Bibliographia Araneorum. 2. Toulouse: Les Artisans de l'Imprimerie Douladoure.

BRYANT, ELIZABETH B.

1940. Cuban spiders in the Museum of Comparative Zoology. Bull. Mus. Comp. Zool., **86** (7): 249-532, 22 pls.

1945. The Argiopidae of Hispaniola. Bull. Mus. Comp. Zool., **95** (4): 359-418, 4 pls.

CAMBRIDGE, O. P.- AND F. P.-CAMBRIDGE

1889-1905. Arachnida-Araneida. Vols. I-II. In: Biologia Centrali-Americana. Dulau & Co., London.

CHICKERING, A. M.

1957a. The genus *Tetragnatha* (Araneae, Argiopidae) in Jamaica, B. W. I. and other neighboring islands. Breviora, Mus. Comp. Zool., no. **68**: 1-15.

1957b. The genus *Tetragnatha* (Araneae, Argiopidae) in Panama. Bull. Mus. Comp. Zool. **116** (5): 301-354, 108 figs.

1959. The genus *Tetragnatha* (Araneae, Argiopidae) in Michigan. Bull. Mus. Comp. Zool., **119** (9): 475-499, 55 figs.

1960. Three new species of *Micrathena* (Araneae, Argiopidae) from South America. Breviora, Mus. Comp. Zool., no. 121: 1-11, 17 figs.

PETRUNKEVITCH, ALEXANDER

1930. The spiders of Porto Rico. Pt. 2, Trans. Connecticut Acad. Arts Sci., **30**: 159-355, 240 figs.

ROEWER, C. FR.

1942. Katalog der Araneae. Vol. 1: 1-1040. Bremen.

SEELEY, R. M.

1928. Revision of the spider genus *Tetragnatha*. Bull. New York State Mus., **278**: 99-150.

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THE ANOLES OF THE EASTERN CARIBBEAN (SAURIA, IGUANIDAE)

Parts IV-VI

BY JAMES D. LAZELL, JR.
and
ERNEST E. WILLIAMS

WITH THREE PLATES

CAMBRIDGE, MASS., U.S.A.
PRINTED FOR THE MUSEUM
OCTOBER 31, 1962

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Proceedings of the New England Zoological Club (octavo) 1899–1948 — Published in connection with the Museum. Publication terminated with Vol. 24.

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No. 9 — *The Anoles of the Eastern Caribbean (Sauria, Iguanidae) Parts IV-VI*

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IV. The Anoles of the Northern Leewards, Anguilla to Montserrat: New Data and a New Species.

By Ernest E. Williams

INTRODUCTION

Initially, as I have stated in the preface to the first part of this series (Williams, 1959), I felt that the Museum of Comparative Zoology collections provided an adequate survey of the anoles of the Lesser Antilles. We had relatively large series of most of the forms recognized, and representatives of all. Many of the specimens were types or syntypes of Garman's or Barbour's names. There were indeed doubts about the application of certain older names, but this was felt to be a purely nomenclatorial problem that could wait upon an opportunity to solve it. There appeared to be very plausible grounds for the belief that a very satisfactory beginning in the revision of the *Anolis* of this limited region could be made by a study of the collections of this one museum — a museum that had a tradition of interest in the region.

As it has worked out, this belief has proved quite wrong. Basic to this error was an assumption that has proved fallacious: the assumption that these small islands could harbor but one or, at a maximum, two species of *Anolis* per island. Where there were as many as two, Barbour had already provided a neat categorization that seemed also an explanation: there were a rupicolous and an arboricolous series.

Underwood (1959) has commented on the taxonomic philosophy of Garman and Barbour which reasoned from the reality of distinct forms on some islands to the existence of endemics on every island. But neither he nor I at the beginning questioned the assumption of extreme faunal restriction and minimal faunal differentiation.

I have now had the opportunity to study many specimens not available to Underwood in the summer of 1957. I have examined the material at the American Museum of Natural History as well as material from the Chicago Natural History Museum, the University of Michigan Museum of Zoology, and also United States National Museum specimens seen by Underwood briefly or not at all. I have received for determination the anoles collected by Walter Auffenberg and J. Wayne King in the Leeward Islands in the summer of 1958. Specimens from Antigua, Montserrat, and Dominica collected in 1958 have been donated to the MCZ by James D. Lazell, Jr. (Over 500 anoles were collected on Dominica by Lazell in 1959. He here publishes separately on the anoles of this island.) Previously I had received live specimens sent up by Underwood in the course of his collections. Kodachromes of some of these are at hand, as well as kodachromes prepared by J. Lazell, Jr., and notes on color in life by Wayne King, Underwood, Lazell, Proctor and others have been available. Live and preserved anoles collected by G. R. Proctor have been repeatedly donated to the MCZ via Underwood. In 1961 National Science Foundation Grant NSF-G16066 provided funds for a Caribbean tour which permitted me to see in the field *Anolis trinitatis*, *A. roquet aeneus*, *A. roquet roquet*, *A. bimaculatus leachii* and *A. wattsi*.

This quantity of previously unreported material supplements Underwood's (1959) presentation, restoring certain names abandoned by him, adding new forms, and hinting at complications still to be recorded. It may be true that the Lesser Antilles provides us with the simplest segment of the genus *Anolis* but this, if it be true, promises tasks in other areas formidable to the point of fantasy. What is here provided is a continuing progress report.

The *bimaculatus* group on the northern islands

Basically the situation seems clear and neat for the members of the *bimaculatus* group in the northern islands from Anguilla to Montserrat. Each bank of the Leewards supports a single

form of the *Anolis bimaculatus* group, and each form is unmistakable on color alone. "Color" is here understood to be color in life; preservation in strong formalin reduces the varied shades present in life to an undistinguished and unpleasant brown and destroys all but the most prominent patterns. Even alcohol loses much of the colors of life and may retain one only — and that not the most frequent — of a repertoire of patterns possible to each individual of a species. I here summarize the presently available evidence for all representatives of the *bimaculatus* group south to Montserrat. I include at the end of each discussion some remarks on the few distinctive scale characters of the several forms, since these were not stressed by Underwood in his presentation: these scale characters are few indeed and modal rather than absolute. I have employed for each form the trinomials used by Underwood, although I have lingering doubts that e.g. *gingivinus* is really conspecific with *bimaculatus*. I find in the case of these island forms, for which the test of sympatry or parapatry is unavailable, the arguments for "splitting" as little compelling or persuasive as those for "lumping." The conventional standard of the degree of difference of valid sympatric forms does not apply in *Anolis*. Forms that in morphology and color are quite distinct may intergrade; forms that are just distinguishable may be full species. I regret that Linnean nomenclature compels decisions which the evidence cannot warrant.

Anolis bimaculatus gingivinus

Notes are available on colors in life for *gingivinus* both in Anguilla and St. Martin. For Anguilla there are notes by both Auffenberg and King on their own collection and also by Underwood for three specimens sent him by G. R. Proctor. I collate their remarks below; I have ventured to combine their slightly varying remarks the more confidently since anoles differ not only from individual to individual but from moment to moment.

Ground color of dorsum dark brown to gray, the gray streaked and spotted with brownish gray or dark brown or with obscure diamonds dorsally. A white or gray stripe from neck above to hind leg. Tail banded with light and dark, sometimes with bronzy sheen at base. Venter light brown or gray. Orbital scales dark brown. Iris black. Dewlap deep yellow orange to umber.

King's description is the only one at hand for St. Martin. He found the *gingivinus* there very similar to Anguilla specimens except that "one was a pale green; none of the Anguilla anoles ever assumed a green color."

This interesting difference in color repertoire may possibly be correlated with a behavioral difference that King noted. For Anguilla, he states: "I noticed a lack of anoles in the trees and bushes — the anoles that I see are always on the rocks or scurrying through the brush. . . . I collected anoles on the hillside north of the salt pond. Almost every large rock not surrounded by weeds had an anole sunning itself on it. The rocks seem to provide the anole with a good view of the surrounding area for they all darted behind the rock no matter what side they were approached from."

In St. Martin, on the other hand, King very specifically mentions catching anoles "from the rocks and trunks of trees." Queried as to this point, he is quite emphatic (letter of March 1, 1959): "Both Dr. Auffenberg and myself feel that the anoles on St. Martin are more arboreal than those on Anguilla. On St. Martin I collected them in trees, bushes and on rocks. To my knowledge I didn't collect a single anole on a tree or bush while on Anguilla. Although I rather doubt it myself, this may be a reflection of the numbers of available trees — Anguilla is very, very scrubby."

The middorsal scales are strongly enlarged in all *gingivinus*, almost as prominent as in members of the *wattsi* group, but in contrast to the conditions in the latter the ventrals in *gingivinus* are quite smooth.

Anolis bimaculatus sabanus

No fresh or live material of this form has come to hand. In this animal, however, the preserved specimens probably give a fairer image of color in life than is true in any other case. The very bold well-spaced spotting (dark brown on light, almost regular), the absence of any flank stripe, and the white belly color are well shown in the alcohol preserved types in the MCZ. The extreme boldness of the pattern is absolutely distinctive, not approached by any other *Anolis*.

There is no enlargement of the middorsal scales in *sabanus;* the ventrals are smooth.

Anolis bimaculatus bimaculatus

I collate below Auffenberg's and King's notes on the color in life of Nevis *bimaculatus*.

Ground color of dorsum yellow green. Flank stripe green or yellow, rarely white. Tail gray or green (blue green) with at

least indications of darker crossbands. Venter yellow white. Head pastel blue or blue green, upper labials and neck yellow. Orbital skin green or light yellowish green. Iris black. A black spot usually present just over front limbs. Dewlap light yellow.

Miss Cochran's (1934) description of a St. Eustatius animal from color notes by Dr. Paul Bartsch is more elaborate:

"The top of the head in front of the eyes is peacock-blue, the larger scales with a pinkish flush that becomes intensified behind the eyes and on the temporal region. The pineal eye is gray brown. The side of the head anterior to the eyes is peacock blue. The area about the eyes is intense brilliant green. The top of the nape is blue with a pinkish flush. The main dorsal part of the body is yellowish green from the nape to the tail. This color extends from the base of the tail over the fore and hind legs, but these have a yellowish pink superimposed, which gradually fades into yellow-green on the belly. On the throat, and from there to the fore leg, are irregularly distributed spots of orange, the posterior portion being uniform in color. The inside of the legs corresponds in color with the belly. The posterior half of the upper side and the outside of the hind legs are marked with obscure spots of blue. An inch behind the base of the tail the same peacock blue seen on the forehead reappears, slowly grading from the general dorsal color. The last two inches of the tail are pale brown. Here spots and splashes of dark brown, blue, and various shades of rose are irregularly scattered about. The median under part of the tail is a little paler than the ground color of the rest, and free from spots on the outer half, the posterior inch of the coarse scaled portion being brown."

Miss Cochran quotes Dr. Bartsch as remarking of Nevis caught *bimaculatus*: "— the blue-green one here is not so beautiful as on St. Eustatius."

King's comments on St. Kitts animals indicate local difference here also: "The yellow shoulder stripe in these lizards is very intense and we saw none in which the stripe was white as in some of the Nevis specimens. They are very large here, some reaching a foot in length and are bluer on the head and tail than the Nevis ones." Underwood has commented that St. Kitts animals are chalky green rather than blue green and that creamy markings are more extensive on the head.

Miss Cochran has commented that the Nevis specimens available to her lacked the shoulder spot characteristic of the animals from St. Eustatius and that the St. Kitts specimens were intermediate — the spot slightly apparent. The reduction or absence

of the shoulder spot in Nevis specimens is very well borne out by the preserved specimens in the MCZ as is the small size of the shoulder spot in St. Kitts specimens. On live Nevis specimens Auffenberg comments, "the large males have a black spot on the body just over the front limbs — however this is quite variable." King states: "There are black spots dorsally and laterally on the back and hind legs and tail. These spots are present only in large males, absent in small ones. Just dorsal to the white shoulder stripe there is a large black spot about the size of the ear opening — one on each side."

In regard to spotting, other than the shoulder spots, preservation produces results very difficult to interpret. In some series the specimens are rather consistently flecked with discrete small spots all over the dorsal surface of head, body and tail. In other series from the same island spotting is inconspicuous or absent. Some formalin preserved specimens show transverse markings and mottlings or even very erratic discolorations. Important as color is in the taxonomy of *Anolis*, it must be used with discretion.

The middorsal scales are somewhat enlarged and sometimes swollen in *bimaculatus* but grade quite gradually into the flank scales. The ventrals are always smooth.

Anolis bimaculatus leachii

Auffenberg provides a color description for *leachii* from Antigua: Ground color light bright green. Tail greenish at base fading into greyish brown over most of its length. Head greyish to brownish speckled or mottled with dark brown or black, "this pattern extending over the shoulders and entire dorsum of some specimens." Dewlap yellowish orange.

Preserved specimens show considerable variability in dorsal speckling and vermiculations. As Underwood has indicated, the spotting tends to coalesce to vermiculations anteriorly but remains discrete posteriorly. Half grown animals appear to show at least occasionally bolder spotting than large adults, but in all cases with much individual variation. (Formalin preservation emphasizes the spotting more than does alcohol preservation; in life also the same individual will show bolder or less bold spotting in different phases.) Sometimes the spots coalesce more or less longitudinally to give the impression of broken lines. In all cases, however, the lower flanks in front of the thighs show no vermiculations and minimal spotting.

Large males have the middorsal scales very distinctly swollen and noticeably but not greatly larger than the adjoining scales. The ventrals are usually smooth.

Anolis bimaculatus nubilus

I have had the opportunity to examine freshly-preserved specimens of this form collected for the United States National Museum. There is, however, no color description from life.

From the preserved animals it is evident that the characters noted by Underwood — almost no trace of flank stripe and light speckling most pronounced in the hind limbs — hold good in the new material. This form seems quite peculiar and distinct in that, at least in preservative, speckling appears to be almost confined to the hind quarters. This is in strong contrast with the Antiguan animal which both in life and in preservation is vermiculate anteriorly — i.e., the speckles are there confluent — and in which even the speckling is reduced posteriorly. The Redonda form is equally different from the Desirade animal in which in all preserved specimens vermiculation is present both anteriorly and posteriorly. The fresh Redonda specimens differ also from the Desirade specimens in the absence of any bright pigment on the orbital scales. In Redonda animals of a general tan body color, these scales are blue gray as preserved.

On the evidence of the new material there is no doubt that the Redonda form is as distinct as is any of the other *bimaculatus* color races, but the lack of knowledge of color in life makes the comparisons incomplete.

The middorsal scales are distinctly larger than the lower flank scales but grade quite gradually into those alongside them. The ventrals are smooth.

Anolis bimaculatus lividus

Underwood has very well described this form. I quote his description with the color variations (or differences in interpretation?) noted by Auffenberg and King in brackets.

"The predominant color is bright yellow green [bright green, pea green] grading to blue [blue green, light blue; "the intensity of the color makes it appear almost fluorescent"] on tail. There is russet [bright orange, red orange] around the eye and a variable extension of russet [brownish, yellowish brown, rust brown] onto the head and forequarters. Oblique rows of pale spots were sometimes present on the sides. The belly is yellow [light yellow to white]. The flank stripe is never strongly defined and is very variable in its extent. These lizards can turn a warm brown [uniform brown, olive]. The fan is light ochre

[light yellow to orange].'' The pale spots on the sides show in a few of the specimens preserved by King. Whether this is a constant character of some specimens or a phase that any individual might sometimes assume, I do not know.

The middorsal scales tend to be enlarged and swollen. The ventrals are weakly keeled.

The *wattsi* series

Specimens of a small anole with strongly keeled ventrals, the keels in line and with two middorsal rows enlarged, are known from Anguilla, St. Martin, St. Eustatius, Nevis, Barbuda and Antigua, unknown on Saba, St. Barts, Redonda, Montserrat, or any isle to the south except for St. Lucia, where this form has only recently been discovered in the port city of Castries (Underwood, 1959, p. 217).

Two nominal species have been described in this series: *A. wattsi* Boulenger 1894 (type locality: Antigua), *A. forresti* Barbour 1923 (type locality: Barbuda). Underwood (1959), without discussing the matter, has placed *forresti* in the synonymy of *wattsi*. In this action he appears to be fully justified; the characters cited by Barbour (1923) in the type description do not hold, and no other characters to distinguish *forresti* and *wattsi* have been found.

Synonymy of *wattsi* and *forresti* is not surprising. The two type localities — Barbuda and Antigua — are islands of one bank with similar ecologies. Underwood was unable (as I am also) to distinguish between the *bimaculatus* representatives on these two islands.

It was somewhat more surprising that the animals from Anguilla, St. Martin, St. Eustatius, St. Kitts and Nevis appeared to be the same as those from Barbuda and Antigua. This was at variance with the situation in the *bimaculatus* group in which each bank had its own well marked form. However, Underwood had seen both the Antiguan and St. Kitts populations in life and had found only trivial color differences. It seemed clear, therefore, when Underwood wrote that *wattsi* was a single form which had undergone hardly any differentiation on the several islands and banks that it inhabited. Underwood, indeed, used *wattsi* as his illustration of ''the process of colonization of a group of islands.'' He said, ''we have the absence from the southeast (i.e., the southern Lesser Antilles) and the slight measure of differentiation between the islands as evidence of relatively recent arrival from the west.''

This conclusion seemed at the time of its writing as plausible to me as to Underwood. It was, therefore, a very real surprise when Auffenberg and King discovered in Barbuda a second species of the *wattsi* group.

Derby Cave, the area in which the new species was first found, was an extremely peculiar habitat — a sink hole in the limestone highlands to the east of Codrington, Barbuda. Wayne King has vividly described the sink hole and its environs:

"The area surrounding the sink hole is scrubby — seldom reaching over twenty feet — woods. Cactus, both "organ pipe" types and low rambling "Opuntia" types are plentiful. Most of the trees and bushes are thorny. There are numerous outcrops of limestone in the area, and very little soil except in

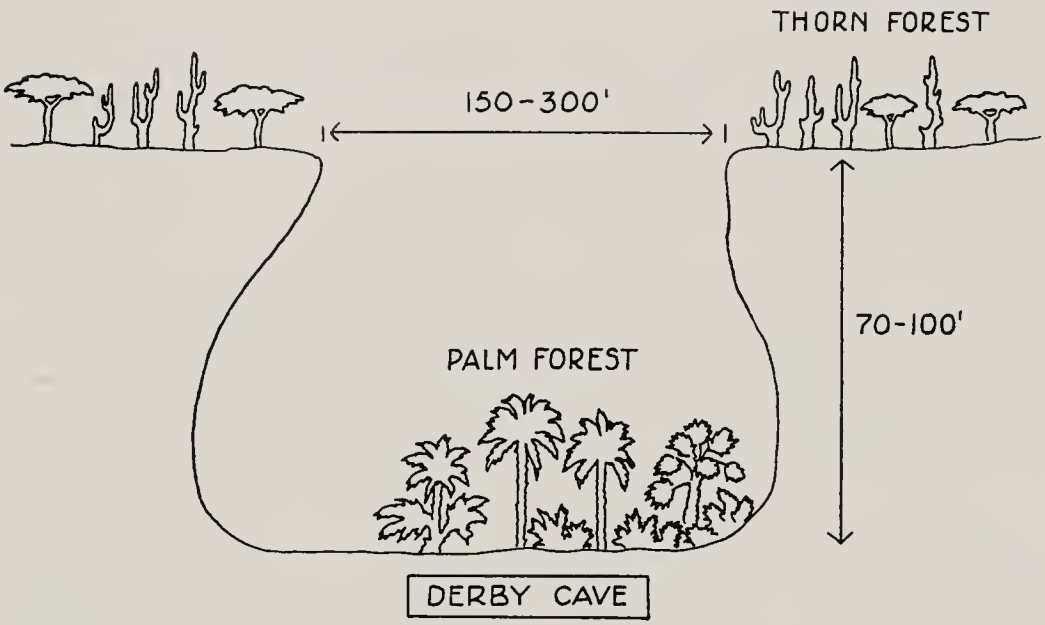

FIGURE 1. Sketch (after field sketch by Walter Auffenberg) of the ecological situation at Derby Cave, Barbuda.

pockets between the outcrops. The sink measures roughly 100 yards across and 80 feet deep. The south side is a sloping pile of rock and rubble; this is the only side which can be used to enter the sink. The other sides, in particular the north side, are sheer drops to the bottom. The north side is overhanging. The bottom of the sink is a loamy clay, dark brown to red in color. There is a dense stand of trees in the bottom. The dominant tree is a palm very similar in appearance to the cabbage palm of Florida, except it is very slender. The trunk of the palm is seldom over six inches in diameter, but trees may be 40 feet tall.

There are many small palms — young ones. Another tree which is abundant is a Ficus — growing mainly on the rock slope on the south side of the sink. The top of the sink is about 150 feet elevation.''

It was on the trunk of the palms that the new species was taken. It was immediately recognized as distinctive on color alone. I compare in parallel columns the color of Barbuda and Antigua *wattsi* and the new species.

wattsi	*new species*
Dorsum greenish brown to brown but base of tail and most of its length translucent yellow or light orange.	Dorsum uniform dark gray or brownish gray or brown to drab olive green.
Top and sides of head including orbital scales translucent yellow or light orange but temples blue gray.	Head without yellow, orbital scales green. No blue gray on temples.
Hind limbs without red markings.	Thighs with red or rusty bands which on the posterior aspect are free of dark overlay and thus appear as brilliant orange spots.
Belly bright yellow.	Belly not yellow.
Dewlap yellowish orange.	Dewlap light green.

The new species was later seen or taken at other localities on Barbuda and Antigua:

1. Dark Cave, 6-7 mi. SE Codrington, Barbuda: anoles seen in shallow sink in which the cave occurs.
2. Bryant Cave, 6-7 mi. SE Codrington, Barbuda: a large sink similar to Derby Cave with a pool of ground water at bottom.
3. Gaynor's Mill, 1 mi. W, 1½ mi. S. Willikies Village, St. Philip's Parish, Antigua: a thick growth of trees with a high canopy growing on the broad flood plain of the river that empties into Nonsuch Bay.

The specimens from these localities differed from those from Derby Cave where the form was first found only in having *white* rather than *red* spots on the posterior edge of the thighs.

The two additional Barbuda localities closely resemble Derby Cave; the Antigua locality is similar in its dampness, high trees and shade.

The color (especially dewlap color) and habit differences reported by Auffenberg and King are in themselves adequate to diagnose the new species. However, the color differences have wholly disappeared in the preserved specimens before me. I have, therefore, strenuously endeavored to find scale differences. I have not been able to find them. Nevertheless, I regard the species status of the new form as unquestionable. Maintenance of sharp color difference, including dewlap color difference, in several small, isolated colonies is for me clear evidence that gene flow does not occur.

As the newly discovered member of a species pair, the new species may receive a Latin name meaning the other one of two and is thus called:

Anolis alter sp. nov.

Type: UF[1] 12457; Derby Cave.

Paratypes: UF 12458-1,2,3,4; MCZ 64345-8, same data.

Referred specimens: UF 12459, Bryant Cave; UF 12460, Gaynor's Mill.

Diagnosis. Closest to *A. wattsi* Boulenger but differing in the absence of yellow on snout and tail, in having a green rather than an orange-yellow dewlap. Differing as well in habitat, being confined to moist shaded areas instead of open dry conditions.

Description. Head scales smooth or at most weakly keeled. Five to seven scales across head at level of second canthal. No frontal depression.

Supraorbital semicircles broadly in contact, partially separated from the supraocular disks by one row of granules on each side. Supraocular disks consisting of *ca.* 5 enlarged scales, separated from the series of overlapping supraciliary scales by 3 rows of keeled subgranular scales. Canthus sharp, canthal scales 5, the first largest, decreasing regularly anteriorly. Loreal rows 4. Temporal scales very small, smallest in center, bounded above by a moderately distinct double line of supratemporal scales. Interparietal slightly smaller than ear, separated from the supraorbital semicircles by two scales, flanked laterally and posteriorly by scales markedly larger than the body scales.

Anterior frontal moderate but less than half the size of anterior supraorbital, separated from the first canthal scale by one scale a little larger than itself.

[1] Florida State Museum, University of Florida, Gainesville.

Four suboculars in contact with supralabials, the subocular series not continued behind the eye, continued forward by two large scales and meeting canthal ridge with no smaller scales intervening. Five to six supralabials to center of eye.

Mentals a little longer than wide, three small granules inserted between their posterior tips. Only one sublabial on each side in contact with the infralabials. Central throat scales small, cycloid, keeled.

Two middorsal rows enlarged, keeled, less than twice adjoining scales which grade gradually into keeled flank scales. Ventrals much larger, keeled, imbricate. Enlarged postanal scales present.

Dewlap scales as large or a little larger than ventrals, keeled, closely packed.

Scales of upper and lower limbs unicarinate, of digits multicarinate. *Ca.* 17 lamellae under phalanges 2 and 3 of fourth toe.

Tail compressed with a strongly enlarged middorsal row of enlarged scales, three per verticil. Lateral scales keeled, large, in 4-5 rows. Ventrally 3 pairs of scales per verticil, somewhat enlarged.

Size: Type, 42 mm snout-vent length.

Comment. Squamation in the *wattsi* group is not by any means uniform. There is variation in the size and crowding of the middorsal enlarged scales, in the degree of keeling, and, to a less degree, in the size of the ventrals. There is also evident variation in the size of the flank scales.

None of these characters, however, appears to be fully useful taxonomically. The size and crowding of the middorsal scales is a sexually dimorphic character: the adult males and females of typical *wattsi* may be accurately sexed by examination of the middorsal scales alone. At one time it seemed possible that *alter* might be distinguished by the less swollen, smaller middorsal scales of the males, more similar to those of females, than in *wattsi.* However, there is a size factor in this sexual difference and when the smaller males of *wattsi* are compared with the available males of *alter* the difference, while probably still real, becomes so subtle as to approach invisibility. The largest male of *alter* is only 42 mm; males of *wattsi* approach 50 mm. There may be a real difference in maximum size here, but the material does not exist to demonstrate the point.

Some of the Nevis specimens of *wattsi* collected by King are near maximum for the species and yet appear to have markedly

smaller middorsals and small flank scales and less keeled ventrals than Antiguan specimens of the same size. Other Nevis specimens, smaller in size (MCZ 38375-6), have significantly larger middorsals and larger flank scales and well keeled ventrals. It is possible that distinct forms are here being confused but without additional information I am compelled to regard the differences as "individual variability."

Color, thus, seems to be the only useful character; the colors in this instance are not likely to be saved even by preservation in alcohol rather than in formalin. Reds and yellows are notoriously fugitive in alcohol and are retained only for a limited period in formalin. The spots on the hinder side of the thighs so much emphasized in the descriptions of live *alter* by King and by Auffenberg are present in all members of the *wattsi* group; they are apparently merely less conspicuous in brown and yellow *wattsi* than in green and red or green and white *alter*. In preserved specimens there is no perceptible difference. A blue tinge appears on the temporal region of Antiguan and Barbudan *wattsi;* this is absent in the *wattsi* of the St. Kitts-Nevis bank. It will, even in preserved specimens, assist in the recognition of *alter* as compared with sympatric Antiguan-Barbudan *wattsi.*

We are left, therefore, with no secure means of telling all preserved *alter* from all preserved *wattsi.* For identification we need data on ecology and on color in life. These are thus true sibling species — since "sibling," here as always, means difficult to tell apart by the *conventional* methods of the taxonomist.

I would, indeed, lack the courage to describe *Anolis alter* if I had not renewed my acquaintance with live *wattsi* by a visit to Antigua in December 1961 and if Walter Auffenberg had not procured for me live *alter* from Derby Cave in March 1962. The color differences which I have listed above for these two species (p. 462) are fully confirmed. The orange so conspicuous on snout, chin, tail and dewlap in live *wattsi* is quite absent in live *alter*. The sole difference which the new collections reveal is that the red spots on the thighs cited for topotypic *alter* in the collections made in the summer of 1958 are in the March-caught specimens of 1962 dull orange. This difference may reflect seasonal changes. At all events it only slightly diminishes the clear-cut difference between the two forms, and is all the less important since *red* markings on the hinder side of the thighs are always absent in non-topotypic *alter*.

V. Geographic Differentiation in *Anolis oculatus* on Dominica

By James D. Lazell, Jr.

In 1956 Garth Underwood collected two series of *Anolis oculatus* in Roseau. Examining these and the specimens already in the Museum of Comparative Zoology he was led to suspect local population differences and therefore concluded in his report (1959) on the anoles of the eastern Caribbean that "clearly Dominica will require further careful examination."

In June of 1958 I was in Dominica specifically for the purpose of collecting some of the larger reptiles for the Philadelphia Zoological Gardens. At that time I collected a number of anoles at several different localities and noted striking differences in these series, apparently correlated with climate and elevation. This collection was donated to the Museum of Comparative Zoology and the following year I returned on behalf of that institution to determine what geographical differences existed and what the relationship of the apparent forms might be. In the course of eight weeks I collected over 500 specimens of this species from thirty localities; it now seems clear that in fact only one species is present but that it divides into four strikingly distinct geographic races.

Anolis oculatus is clearly a member of the *bimaculatus* group of Lesser Antillean anoles. (I follow Underwood [1959] in treating it as a distinct species.) It averages much smaller than *bimaculatus* (adult males: 70-76 mm snout to vent — except in the upland race, which approaches *bimaculatus* with lengths of up to 96 mm), and possesses weakly keeled ventrals and a double row of enlarged, sometimes swollen, middorsal scales. Generally the scales are convex, particularly on the head and neck. All forms show caudal cresting in the adult males and in some this is pronounced. Males also have an extensible nuchal crest.

Coloration and pattern vary widely within the species and furnish the principal basis for differentiation of the forms. The species as a whole shows a greater or lesser amount of spotting; from this feature the trivial name is derived. The spotting consists of alternating primary and secondary vertical rows of light spots — generally three to five of each along each side of the animal. The primary rows have their spots accentuated by dark, often black, pigment areas in the adult males; these dark pigment areas may be borders on several primary spots, or dots

or flecks surrounding or adjacent to a few primary spots, or large black patches forming a background for a number of primary spots and extending so as to nearly include the secondary rows. In one form the dark pigment areas may be occasionally completely lacking; in general this dark pigmentation is more pronounced on the larger male specimens and absent completely on the young and the half grown.

In ecology and habits *A. oculatus* seems plastic. It utilizes almost any available habitat from sea level to nearly 3000 feet. It appears, however, to be much more common in some areas than others. Along the Trans-Insular Road between Bells and Concord, for example, a distance of some ten miles, repeated trips resulted in the capture of only one specimen. In the same type of habitat and at similar elevations in other areas I had no trouble securing series. From just south of Roseau and just south of Point Mulatre an imaginary line can be drawn, south of which any anole is hard to come by, whatever the elevation or habitat one seeks them in. Why anoles should be so abundant in places like Roseau, the Fresh Water Lake, the Cabrits or Woodford Hill — each locality possessing a different form — and so scarce in certain other localities I leave to further investigation. Generally, however, the species is abundant enough so that several series of each form could be taken without difficulty and intermediate populations collected also.

This is a lizard with a preference for only vertical stations; it does forage on the ground and seldom ascends to a height of more than a few yards, but it seems to prefer sitting on a vertical substrate — whether it be a tree, bush, wall, road-cut, stone or building. It will occasionally seek shelter under stones, or between them, or in root masses if pursued. Further discussion will be found under the subspecies. (For distribution of subspecies see map, Plate 3.)

Anolis oculatus oculatus (Cope)

Xiphosurus oculatus Cope, 1879. Proc. Amer. Phil. Soc. **18**: 274.
Cotypes: USNM [1] Nos. 10139-48, 10150-1, 10153. Type locality, Dominica. Coll. Ferdinand Ober.

Cope's description does not mention a definite locality within the island, and the type series contains specimens that show occasional similarities to the northern Leeward coast form. Perhaps

[1] United States National Museum.

Ober's collection is composite, or represents an intermediate locality. However, most of the specimens described by Cope fit reasonably well with the southern coastal form, and some, like USNM 10145, closely resemble our figure of MCZ 60364 from Roseau. Thus it seems advisable to restrict the type locality to Roseau, the principal seaport of the island. The following is a description of fresh material collected by me.

Diagnosis. Ground color olive to tan; venter dirty yellow to whitish. Spots, both primary and secondary rows, less distinct than in ony other form and sometimes completely lacking. Black pigmentation adjoining spots very reduced or absent.

Coloration in life of adult males. (MCZ Nos. 60359-408, Roseau; coll. J. Lazell, 8 August, 1959.) Extremely variable; most specimens mottled olive or tan with dirty yellow venters and a yellowish tinge on the sides. Most specimens show at least a few spots in the primary rows; these are indistinct and show up best when there are black flecks or patches surrounding them; these patches occur in the majority of specimens around one to two, occasionally three, primary spots. In some specimens there is no black pigment present and in a few the primary spots have become so indistinct that the animal appears solid colored. The secondary spot-rows are generally faded to mere mottling between the primary rows. There is little if any marking on the head and neck and no distinctive coloration on the skin around the eye. (Top, Plate 1.)

Throat fan. Pumpkin yellow to orange.

Color of females and juveniles. Light olive to tan with whitish venters. Spots, if present at all, are very indistinct. There is usually a distinguishable dorsal stripe and often a lateral streak.

Additional series. MCZ Nos. 60425-40, Second Layou River Bridge, above Hillsborough; MCZ Nos. 60350-8, Hillsborough; MCZ Nos. 60409-14, Pointe Michel; MCZ Nos. 60415-24, Grand Bay. All of these specimens agree on all characters except that in the Grand Bay series there are no large adult males and no specimens showing any dark pigment areas.

Discussion. The southern leeward coast of Dominica is semi-xerophytic; this zone rounds the southern tip of the island and extends northward as far as the 1600 foot barrier of Morne Paix Bouche. This mountain, placed exactly on the coast, separates the drier area to the south from the wet lowlands or transitional forest of the windward coast to the north. Thus it is from just south of Morne Paix Bouche, around the southern tip and then

northward to the Layou Valley, that the nominate form of *Anolis oculatus* occurs. MCZ Nos. 60683-4, from Morne Paix Bouche, are almost typical *oculatus;* they differ somewhat in having more spotting than is usual and a richer, browner ground color. Thus I have considered them intergrades with the form of the more northern windward coast.

Caudal and nuchal crests are present in *A. o. oculatus,* but less evident than in any other form.

This is the smallest subspecies, the largest male measuring 73 mm snout to vent.

Anolis oculatus cabritensis subsp. nov.

Type. MCZ No. 60245, the Cabrits (= Prince Rupert Point), northwest of Portsmouth, Dominica. Coll. J. Lazell, 8 June, 1959.

Diagnosis. Ground color grey to pale tannish; venter bright yellow to pale peach color. Primary spots large, bold and well separated; secondary spots running into stripes. Black pigmentation enclosing several spots.

Coloration in life of adult male type and paratopotypes (males from series MCZ Nos. 60207-54). Very pale ash grey to tan; venters yellow to pale peach. Primary spots very large and bright; in most specimens they are blue — varying from sky blue to merely a faint blue-grey. These primary spots form two to three, occasionally four, extensive black pigment areas, corresponding to the primary spot rows. Each black patch contains from two to three primary spots and sometimes extending so far as to nearly surround the secondary spots. The secondary spots are less bright but quite bold and large and well run together, forming vertical stripes on most specimens, particularly posteriorly. The head and neck are stippled with whitish spots and streaks; the skin around the eye is the same color as this stippling. In nearly half the specimens the head has a very wine-red cast, particularly anterior to the eyes. In all cases the snout is at least browner than the ground color. (Bottom, Plate 1.)

Throat fan. Light bright yellow.

Color of females and juveniles (paratopotypes from series MCZ 60207-54). Pale grey ground color; venters yellowish. More spots and these more run together than in any other form. Dorsal and lateral striping also bolder.

Additional paratypes. MCZ Nos. 60299-317, Picard. This series, from a wetter area, is somewhat darker and more yellow than the Cabrits specimens; otherwise it agrees on all characters.

MCZ Nos. 60255-75, Pointe Ronde. These agree with the Cabrits series on all characters, but show slightly more yellow along the sides.

MCZ Nos. 60276-98, Grand Savanna. This series differs from the Cabrits specimens on no diagnostic characters, but shows a definite tendency for the bright yellow of the venter to invade the dorsal ground color — though it remains basically pale grey. There is much less evidence of red on the head anterior to the eyes, though this area is still generally browner than the rest of the ground color.

Discussion. The leeward coast of Dominica from the Grand Savanna to the Cabrits is the driest part of the island. Largely, it is truly xerophytic. This is the habitat of this palest, most boldly marked subspecies. In the wetter zones, like Picard, the population approaches the tan extreme of ground color. To the north *cabritensis* intergrades with the windward coast form (see below). Animals from the southern part of the range are brighter yellow and the yellow invades the dorsal ground color; in the northern part of the range there is a tendency toward red on the top of the head that is considerably less frequent in the southern population. In the male the heavy, bold spotting, large black pigment areas and stippling on the head and neck serve to distinguish this form immediately. Young and females are distinguished with equal ease by their pale grey ground color and large, bold markings.

This form shows the greatest degree of caudal cresting; the nuchal crest is also very well developed.

In size this seems to be the second largest — the biggest male measuring 75 mm snout to vent.

Anolis oculatus montanus subsp. nov.

Type. MCZ No. 60319, Fresh Water Lake, *ca.* 2500 feet. Coll. J. Lazell, 6 July, 1959.

Diagnosis. Ground color from light to dark green; venter paler green to rather bright metallic green. Spots small and bright; primary rows with spots larger and further apart, secondary rows with spots smaller and close together. Black pigmentation in one or more patches surrounding spots of primary row.

Coloration in life of adult male type and paratopotypes (males from series MCZ 60318-37 and 65919-48). Ground color from light leaf green to dark slatey green; venter paler green and dingier. Spots in irregular but recognizable rows — those of the

primary rows may have some (one to two — occasionally three) black patches surrounding one or two of the spots on each of the anterior rows. All spots rounded in shape and from white to lime green in color. Spotting extends profusely onto the head and neck — often well onto the ventral surface. Skin around eye sea green. (Top, Plate 2.)

Throat fan. Dark yellowish suffused with rusty brown. Scales light green.

Color of females and juveniles (paratopotypes from series MCZ 60318-37). Ground color green; venter often metallic looking. Spots small and fairly profuse. Fans dark brick-red. Dorsal stripe and lateral streak usually present.

Additional paratypes. MCZ No. 60338, Gleau Gomier, at the Old Carib Trace, *ca.* 2000 feet. MCZ Nos. 60339-49, Fond Hunt, *ca.* 2000 feet. These series agree in all characters with the topotypic series.

Discussion. This form is found throughout the central mountain range in rain forests over 2000 feet, approximately, and up to nearly 3000 feet. Evidence of its genetic influence can be found in the presence of greener coloration in surrounding populations at elevations above 800 feet. From this level spotting changes clinally upward until it becomes consistent as that characteristic of the montane subspecies at about 2000 feet. It is interesting to note that no evidence of *montanus* influence exists in the specimens taken on Morne Paix Bouche, *ca.* 1600 feet, on the coast, and thus the distance inland seems to be a factor as well as the elevation itself. The northern high point of the island, Morne au Diable, provides a series taken between 2000 and 2500 feet. These animals show definite *montanus* characters, but more closely resemble the windward coast form. This highland area is separated from the main ridge of mountains on the island by a gap that is little higher than 200 feet. Specimens taken at Dos D'Ane, at the high point of the gap, *ca.* 200 feet, show no evidence of *montanus* influence; the population on Morne au Diable is thus separated from the rest of the *montanus* range and surrounded by the windward coast form and its intergrades with *cabritensis.*

In this subspecies the tail crest is usually well developed but the nuchal crest is as little in evidence as in *A. o. oculatus.*

This is certainly the largest subspecies; a number of adult males measure between 76 and 85 mm. snout to vent and one, MCZ No. 60344, from Fond Hunt, is probably the largest *Anolis oculatus* ever collected — measuring 96 mm snout to vent.

ANOLIS OCULATUS WINSTONI subsp. nov.

Type. MCZ No. 60467, Woodford Hill. Coll. J. Lazell, 29 June, 1959.

Diagnosis. Ground color coffee; venter deep peach to bright yellow. Little distinction between primary and secondary spots; spots tend to be rounded in outline and small to moderate in size. Black pigmentation rudimentary, at most dark borders to the spots.

Coloration in life of adult male type and paratopotypes (males of series MCZ Nos. 60441-90). Ground color coffee, varies from light to dark. Venter usually deep peach, sometimes shading to bright yellow. The animals are heavily peppered with small to moderate sized white dots that often have some indication of dark bordering, though never the black patches found in the other forms. There is little if any distinction between primary and secondary spot rows in most specimens. Spots extend heavily onto the head and neck; skin around eye varies from white to sky blue. (Bottom, Plate 2.)

Throat fan. Deep pumpkin yellow.

Color of females and juveniles (paratopotypes from series MCZ 60441-90). Ground color coffee, sometimes with faint olive tint. Spots less obvious than in adult males and somewhat obscured by longitudinal streaking.

Additional paratypes. MCZ Nos. 60491-507, Penville; MCZ Nos. 60508-20, Blenheim; MCZ Nos. 60640-4, Hatten Garden; MCZ Nos. 60521-4, Salybia; MCZ Nos. 60525-38, Castle Bruce; MCZ Nos. 60539-50, Rosalie; MCZ Nos. 60622-39, La Plaine. All agree with the topotypic series in all characters.

Discussion. This form has the widest range of the four, being found in the transitional forests or wet lowlands all along the windward coast from the northern point, Penville, to the barrier of Morne Paix Bouche, south of which the country becomes drier. Specimens taken at Pointe Mulatre, just north of Morne Paix Bouche, fit *winstoni* well, but are paler and more olive with spotting less distinct; this then is the zone of intergradation with the nominate form. *A. o. winstoni* intergrades with *cabritensis* at Dos D'Ane, between the central massif and Morne au Diable, and on the northern coast as far south as the Cabrits peninsula. It intergrades with *montanus* on Morne au Diable and undoubtedly all along the eastern slope of the Morne Grand Bois-Diablotin massif. Ecologically, then, this is the form of the wet lowlands.

The nuchal crest is more pronounced in *winstoni* than in any other form, though the caudal crest is not usually so well developed as in *cabritensis*. There is a tendency in old males for the scales within the white dots to become swollen and tubercular; this occurs to slight extent in both *montanus* and *cabritensis* in occasional specimens; this never occurs in *oculatus*. In no case, however, is it as pronounced or common as in *winstoni*.

In size this form falls between *oculatus* and *cabritensis*, with the largest male measuring 74 mm snout to vent.

This subspecies is named for Charles A. Winston, Manager of Woodford Hill Estate, and his family. His knowledge of the island's wildlife and his constant willingness to assist me in my wanderings over the island made possible the collection here reported.

Discussion

There are several additional series of *Anolis oculatus* which are pertinent to the discussion of this animal. These include MCZ No. 28593, Roseau; coll. Thomas Barbour, 1929. This specimen is badly faded, but shows the black pigment areas well and these would definitely relegate it to the subspecies *oculatus*. MCZ Nos. 55706-8, Rouseau; coll. G. Underwood, 28 July, 1956 — also typical *oculatus*. MCZ No. 59162, near Fresh Water Lake, *ca.* 2000 feet; coll. Dr. Joseph Seronde, 3 July, 1959. This specimen is apparently a typical young *montanus*. Two other series present difficulty:

MCZ No. 6160 (24), Roseau; coll. S. Garman, 1879. This appears to be a series of specimens intermediate between *oculatus* and *cabritensis*, possibly from the coastal area around St. Joseph or Machouchery, eight or nine miles from Roseau. In fact, this series agrees quite well with my own from Machouchery (MCZ Nos. 60645-54) which are intermediate in characters. This area is close enough to Roseau so that it seems feasible that the series in question could have been collected there; in fact, since the large estates on the island were in this area, it seems quite probable that Garman headed in that direction. (Note that some of Cope's type series seem intermediate in the same way but to a lesser degree.)

The second series, MCZ No. 6159 (14), Portsmouth, coll. S. Garman, 1879, is more difficult to interpret. Three appear to be *winstoni* × *montanus* intergrades, possibly from the hills to the

northeast of Portsmouth; proceeding in this direction the influence of the coastal *cabritensis* is quickly lost. Eight are so badly faded that at first they suggest *oculatus* of the south coast; this I believe is entirely due to the fading though, for where any indication of spotting remains it would indicate some head markings, making a northern locality likely. The three remaining juveniles are badly discolored and cannot be assigned to any particular form. It seems at least plausible that all of these came from the hills above Portsmouth.

Garman states in his account of these animals (1887) that they were taken "at several points on Dominica," though only two localities appear on the labels. He includes a description of them that certainly fits the species, but which cannot be assigned to any one of the subspecies.

Possibly these old collections serve to emphasize the remarkable differences that can take place on an island like Dominica within a relatively small area — literally within a comfortable walk! The island is only twenty-eight miles long and approximately seventeen miles wide and it may at first look seem strange that subspecies differentiation could take place on it at all. However, when one considers that Dominica's central highlands rise to nearly 5000 feet in several places and that the prevailing wind direction is constantly from the northeast then the wide differences that exist in habitats and ecologies become clearly explicable.

The top and windward side of the island are blanketed with rain forest nearly down to sea level, where cultivation has not cleared the original vegetation. Along the windward coast is a broad transitional zone, which gives way on the leeward coast and southern tip to semixerophytic and xerophytic dry scrub woodlands and cactus country. The coast that lies in the lee of the huge massif of Morne Diablotin is virtually deprived of any rainfall — at least by comparison with the country to the windward of it.

The floral ecology of Dominica then divides into strikingly different zones that correspond remarkably with the distributions of the four geographic races of *Anolis oculatus* (Hodge, 1954).

In summation, it seems evident that the differing ecologic zones on a single island, such as Dominica, are more effective in differentiating forms of reptile life than are barriers, like water expanses, between islands of similar ecology. We need only compare Dominica with Antigua and Barbuda in the Leeward Islands to the north: even between these islands separated by

forty miles of sea there is little if any noticeable difference in the *Anolis* population. Both are low, dry islands with only pockets of wetter vegetation. Ecologically the two are virtually the same — a far cry from the situation that obtains in moving from one side of the island of Dominica to the other.

TABLE OF DIAGNOSTIC CHARACTERS
in
Anolis oculatus Subspecies

	oculatus	*cabritensis*	*montanus*	*winstoni*
Throat fan color	Pumpkin yellow	Light bright yellow	Dirty reddish	Pumpkin yellow
Dorsal spotting (white)	Indistinct primaries; Secondaries mere mottling	Large, bold primaries; Secondaries bold, run together	Small, round alternating primaries and secondaries	Small, bold; little differentiation
Black pigment areas	Variable; small — 0 to 3 present	Large; extensive, 2 to 4 present	Small; 1 to 3 present	Reduced to mere dark bordering
Ground color	Olive to tan	Pale grey to tan	Green	Coffee
Venter color	Dirty yellow to white	Yellow to pale peach	Green	Peach to bright yellow
Tail crest	Low	High	Moderate	Moderate
Size (maximum) (snout to vent)	73 mm	75 mm	74 mm	96 mm

VI. Species and Ecology

By Ernest E. Williams

Anolis oculatus and its races, and the sibling pair *Anolis wattsi*—*A. alter* emphasize the strong correlation of *Anolis* species with ecology. A parallel case is provided by the brown and green races of *Anolis lineatopus* (Underwood and Williams, 1959).

It is very instructive to contrast the races of *A. oculatus* with *A. wattsi* and *A. alter*. In *A. oculatus* it is conspicuous that gene flow is even now occurring between strongly marked races adapted to sharply distinct ecologies. Relatively narrow zones of intermediate ecology permit the existence of intermediate populations that still effectively bind this heterogeneous assemblage into a single gene pool.

In the case of *alter* and *wattsi*, intermediate ecologies are absent and the thread of genetic continuity seems to be broken also. It is tempting to suppose that—by analogy with the *oculatus* races—*alter* and *wattsi* differentiated on the Antigua-Barbuda bank in wet and dry zones respectively, that with the climatic deterioration which occurred in the late Pleistocene (Richard Howard, personal communication)[1] the wet areas have been reduced to sharply set off highly peculiar disjunct oases on islands that are primarily arid. Thus *A. alter* would be confined—as it seems to be—to these singular remnants of wet forest—tiny "lost worlds." The gene flow that had existed between the subspecies *wattsi* and the subspecies *alter* would have progressively diminished with the contraction and ultimate disappearance of the intermediate zones between wet and dry ecologies. In such a way it might be believed that *alter* and *wattsi* have achieved that genetic independence which currently appears to define their species status.

But the evidence does not at the moment permit us to exclude other possibilities. *A. wattsi* occurs not only on the Antigua-Barbuda bank but on the St. Kitts-Nevis-St. Eustatius bank and

[1] The former more favorable ecology of Barbuda is demonstrated also by the fossil fauna found there by Walter Auffenberg (1958). An extinct *Hyla* and an extinct representative of the snake *Pseudoboa* are cited by him.

on the St. Martin-Anguilla-St. Barts bank as well.[1] While *A. wattsi* may have spread out from Antigua to these other islands very recently, no present evidence negatives the alternative that it has recently invaded Antigua-Barbuda from elsewhere. In this case *A. alter* might be the autochthonous element on Antigua and Barbuda, and *A. wattsi* the invader that has seized the dry island areas that wet-area adapted *A. alter* held but weakly or not at all.

We cannot now choose among these and other hypotheses but the dominant role of ecology and ecological change in the history of *Anolis* species in the Antilles is already strongly highlighted.

[1] The occurrence on St. Lucia (Underwood, 1959) may be a case of human transport.

REFERENCES CITED

(Parts IV-VI)

Auffenberg, W.

1958. A small fossil herpetofauna from Barbuda, Leeward Islands, with the description of a new species of *Hyla*. Quart. J. Florida Acad. Sci. **21**: 248-254.

Barbour T.

1923. West Indian investigations of 1922. Occ. Pap. Mus. Zool. Univ. Michigan No. 132: 1 7.

1930. The Anoles. I. The forms known to occur on the neotropical islands. Bull. Mus. Comp. Zool. **70**: 105-144.

Cochran, D.

1934. Herpetological collections from the West Indies made by Dr. Paul Bartsch under the Walter Rathbone Bacon Scholarship, 1928-1930. Smithsonian Misc. Coll. **92** (7): 1-48.

Cope, E. D.

1879. Eleventh contribution to the herpetology of tropical America. Proc. Amer. Phil. Soc. **18**: 261-277.

Garman, S.

1887. On West Indian Iguanidae and on West Indian Scincidae in the collection of the Museum of Comparative Zoology at Cambridge, Mass., U.S.A. Proc. Essex Inst. **19**: 25-53.

Hodge, W. H.

1943. The vegetation of Dominica. Geographical Review **33**: 349-375.

1954. Flora of Dominica, B.W.I. Part I. Lloydia **17**: 1-238.

Underwood, G.

1959. Revisionary notes. The anoles of the Eastern Caribbean (Sauria, Iguanidae). Part III. Bull. Mus. Comp. Zool. **121**: 191-226.

Underwood, G. and E. E. Williams

1959. The anoline lizards of Jamaica. Bull. Inst. Jamaica Sci. Ser. **9**: 1-48.

Williams, E. E.

1959. Preface. The anoles of the Eastern Caribbean (Sauria, Iguanidae). Part I. Bull. Mus. Comp. Zool. **121**: 187-189.

PLATE I. Top: *Anolis oculatus oculatus*, MCZ 60364, midbody. Bottom: *Anolis oculatus cabritensis* subsp. nov. Type, MCZ 60245, midbody.

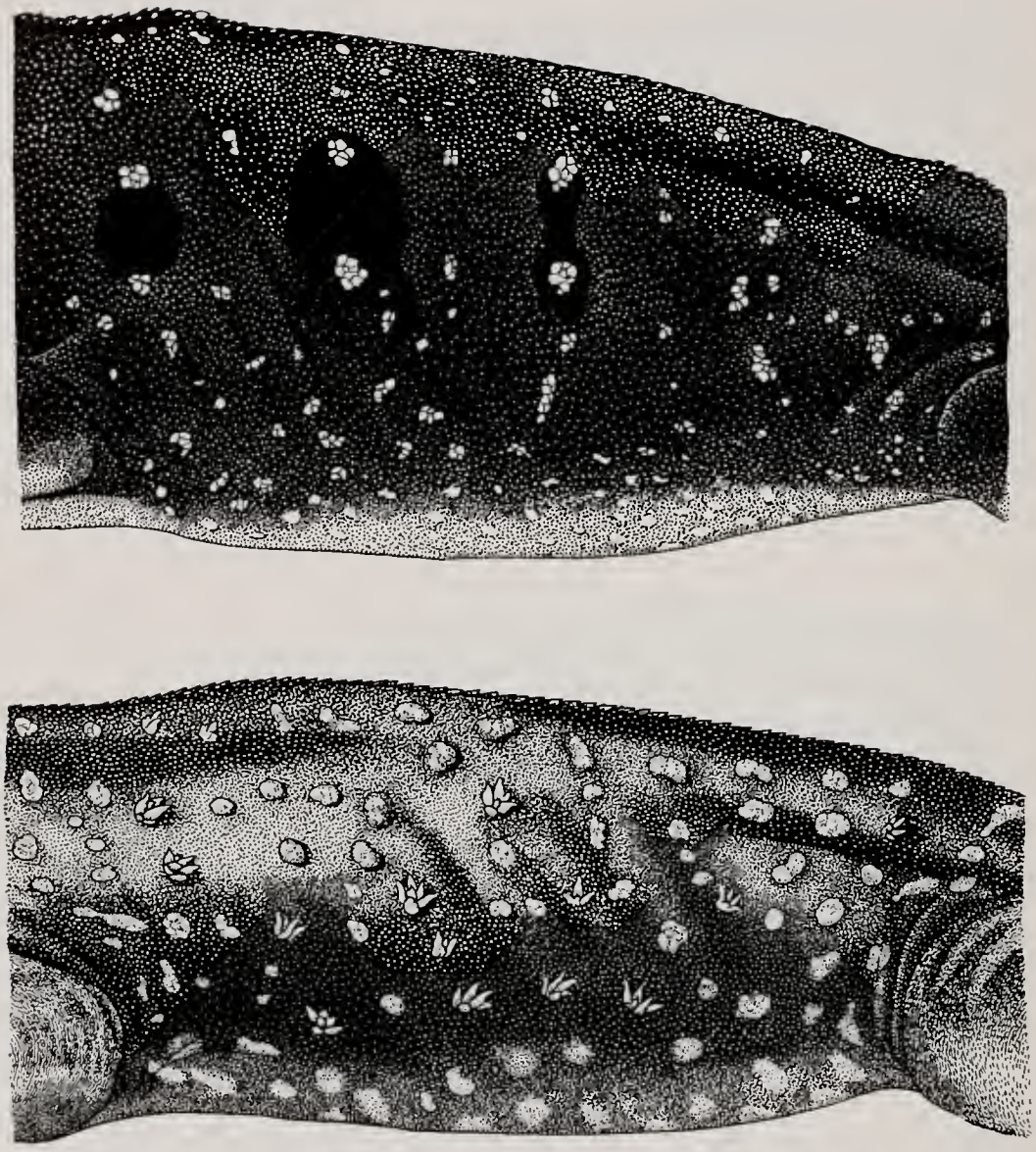

PLATE 2. Top: *Anolis oculatus montanus* subsp. nov. Type, MCZ 60319, midbody. Bottom: *Anolis oculatus winstoni* subsp. nov. Type, MCZ 60467, midbody.

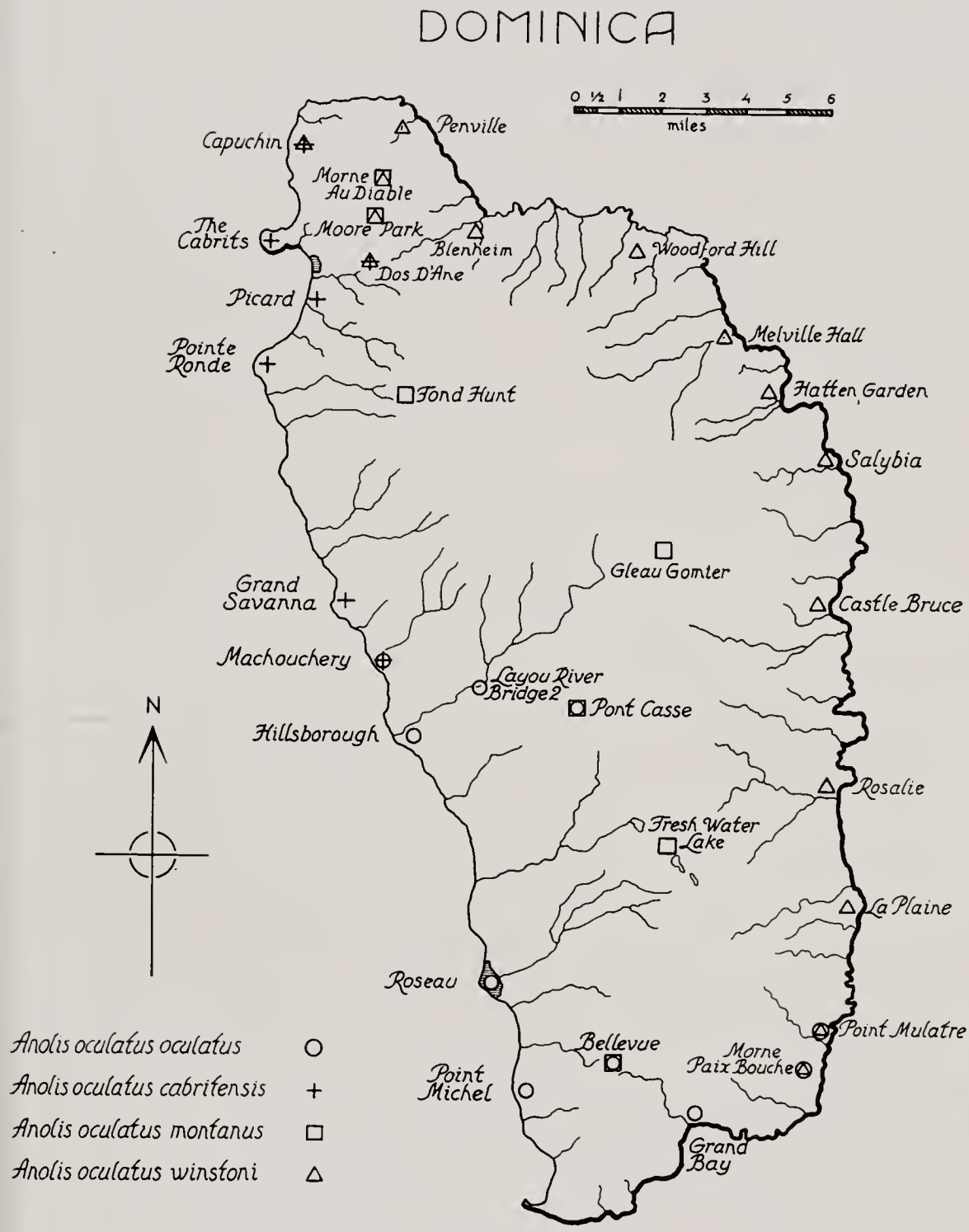

PLATE 3. Distribution of *Anolis oculatus* subspecies.

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JAMAICAN AND HISPANIOLAN GONATODES AND ALLIED FORMS (SAURIA, GEKKONIDAE)

By Paulo E. Vanzolini
Departamento de Zoologia
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and

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Cambridge, Massachusetts

CAMBRIDGE, MASS., U.S.A.
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Johnsonia (quarto) 1941 — A publication of the Department of Mollusks. Vol. 4, no. 41 is current.

Occasional Papers of the Department of Mollusks (octavo) 1945 — Vol. 2, no. 28 is current.

Proceedings of the New England Zoological Club (octavo) 1899–1948 — Published in connection with the Museum. Publication terminated with Vol. 24.

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Memoirs: Requests for some specific memoirs can be filled but no list is available.

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No. 10 — *Jamaican and Hispaniolan Gonatodes and Allied Forms (Sauria, Gekkonidae)*

By Paulo E. Vanzolini and Ernest E. Williams

INTRODUCTION

Lizards of the genus *Gonatodes* are known in three of the Greater Antilles: Cuba, Jamaica and Hispaniola. Those from the former two islands have been assigned to *G. fuscus,* a form otherwise known from Colombia and Central America, while Hispaniola has been credited with an endemic species, *G. notatus.*

A preliminary survey showed that, on the basis of qualitative scutellation characters and female (and juvenile) color pattern, the three insular populations were not distinguishable from one another nor from continental *G. fuscus* nor from what has been called in Colombia and Venezuela *G. albogularis.* On the basis of adult *male* color pattern, however, three groups could be easily distinguished: (a) continental and Cuban *fuscus;* (b) Colombian and Venezuelan *albogularis;* (c) Jamaican *fuscus* and Hispaniolan *notatus,* much closer to *b* than to *a.*

In the present paper an attempt is made at clarifying the relationships of South American *fuscus* and *albogularis* (particularly in Colombia) and then, with aid of the information thus derived, of the Jamaican and Hispaniolan populations. It is hoped that in the future it will be possible to proceed with a study of Central American and Cuban *fuscus.*

ACKNOWLEDGMENTS

We are indebted to the following persons and institutions for the loan of specimens: Charles M. Bogert, American Museum of Natural History, New York; Norman Hartweg, University of Michigan Museum of Zoology, Ann Arbor; Hermano Niceforo Maria, Instituto La Salle, Bogotá; Jean Guibé, Muséum National d'Histoire Naturelle, Paris. For the privilege of examining a large series of *G. notatus* from Gonave Island we are indebted to Dr. P. S. Humphrey, Peabody Museum, Yale University, who collected this material during a Yale-Florida expedition to Haiti in the spring of 1959. Some additional Haitian material

has been obtained for the Museum of Comparative Zoology under NSF grants G 5634 and G 16066.

The senior author wishes to express his gratitude to the John Simon Guggenheim Memorial Foundation and to the Brasilian Conselho Nacional de Pesquisas for financial support of his work on South American lizards.

GENERAL DESCRIPTION OF THE *GONATODES ALBOGULARIS* COMPLEX

The following description applies to both *fuscus* and *albogularis* and indeed to all members of this complex:

Rostral low, not very broad, slightly nicked superiorly, with a median sulcus but not depressed. Nostril surrounded by the rostral, one infra-nasal, two post-nasals and one narrow supranasal, separated from its fellow. Snout granules prominent, decreasing posteriorly. Superciliary granules moderately to inconspicuously aculeate. Supralabials 6, anterior largest, reaching the middle of the eye. Temporal granules as large as the parietal ones. Infralabials 5 (first very large), reaching the same level as the supralabials. Symphysial large, followed by a transverse row of 6 enlarged gulars, the outermost on each side sometimes displaced backwards. Gulars very small, smooth, juxtaposed, grading posteriorly into granules and then into the ventrals.

Dorsal granules somewhat smaller than those on the snout. Ventrals as large as 3-4 dorsal granules, smooth, oval, imbricate. Forelimb dorsally, hindlimb ventrally with smooth scales, elsewhere granular. Toes in the following order of decreasing length: 4, 3, 2, 5, 1. Ventral lamellae of third finger 14-20, of fourth toe 18-22.

Tail dorsally granular, ventrally with juxtaposed to subimbricate scales, those of the median row 2-3 times wider than the others.

GONATODES ALBOGULARIS AND *FUSCUS* IN COLOMBIA

The forms currently called *Gonatodes albogularis* and *fuscus* appear to be, at least broadly speaking, sympatric in Colombia and adjacent Venezuela. An investigation of the present complex may therefore very usefully begin by an analysis of their mutual relationships in this region.

Character Analysis

Color pattern: general.

Before discussing color patterns, it should be noted that we have ourselves dealt *entirely* with preserved specimens. In the case of juveniles and females, where browns and greys are prevalent, we doubt whether the observation of live animals would add new elements. In the case of adult males, however, it is certain that preservation entails loss of much information. There is, for instance, no warrant for belief that the pure white of the throat of preserved *albogularis* is white in life — *in fact, it is known that it is not* — nor that throats showing the same color in the collection bottle did so in nature. Again, the question of the presence or absence of a specially pigmented area on the sides of head and neck is especially tantalizing since this pigment is inconspicuous or absent in preserved specimens, an unusual thing for a secondary sex character.

Color pattern: females and juveniles.

Dorsal ground color gray, with darker marblings or reticulations, usually tending to form chevrons on the nape, and pairs of spots on the dorsum. The vertebral region lighter. Ventral parts yellowish, with small dark punctuations.

Color pattern: adult males.

Two major male patterns are evident.

1. The name *albogularis* has been applied to males with the following color pattern in preservation: Dorsal parts and flanks dark, from dull gray to almost black, the color invading the sides of the belly to a variable extent. A dark vinaceous spot from the lips to the sides of the neck, sometimes reaching the shoulder, sometimes interrupted in the middle. Throat dead white, the color extending, less pure, on the chest. Escutcheon, ventral surface of thighs and base of tail almost white. Connecting the thoracic and lower ventral light areas, an irregular light streak, more or less narrowed or even interrupted by the dark color of the sides of the belly.

2. Males to which the name *fuscus* has been applied have also a dark dorsum. The whole head is sometimes lighter, pinkish, resulting in a "hooded" aspect. The ventral parts are tan or somewhat darker, the throat dirty pink, with more or less distinct gray chevrons. The escutcheon and thigh are a little lighter than the remainder of the venter.

In assigning our specimens to either color pattern, we were forced to adopt a unilateral criterion. The *albogularis* extreme in the range of male pattern is very clear. There is, however, a gradation towards darker throats, with more or less distinct chevrons, and less conspicuous ventral markings. In preserved specimens, at least, it is impossible to define an extreme *fuscus,* or to accurately grade the intermediates. (It should be remembered that we are attempting to evaluate color in specimens preserved in many different ways at many different times.) In what follows we have used the name *albogularis* for the specimens agreeing perfectly with the description under this name above. All other male specimens have been regarded as having the *fuscus* coloration, irrespective of variation. The "hooded" character was too variable after preservation to be taken into account.

Geographical distribution of color patterns.

Inspection of Table 1 and the map shows that the *albogularis* male pattern is found in a strip of territory extending from the middle Magdalena (Honda) to Merida in Venezuela, with highest incidence in the valley of the Zulia (Cucuta). Fairly large samples from the lower Cauca (Sabanalarga) and from the Atrato (Quibdó) drainages make it rather safe to say that in western Colombia only the *fuscus* pattern is found. Surrounding the central core of pure *albogularis* male pattern (Cucuta and San Gil) there are mixed samples (Merida and Honda).

This distributional pattern is compatible with the hypothesis of two subspecies. In fact, it would be common taxonomic procedure to accept the hypothesis on only these grounds. We prefer to believe, however, that subspecies should be based on a *reasonably* (not absolutely) concordant distribution of uncorrelated characters coinciding (again to a reasonable degree) with broad ecological patterns. In the case at hand, we have at present no means of testing the latter aspect, but it has been possible to investigate one quantitative character for its correlations with the male color patterns.

Quantitative characters: general.

Searching for characters that could be expressed numerically, we first tried the number of infradigital lamellae of the third finger and of the fourth toe, counts which have been found useful in other forms in the genus. In the present case, however, they proved very weakly, if at all, discriminative.

On the other hand (as suggested by Stejneger, 1917), the size of ventral scales seemed to show geographical differentiation, western samples (*fuscus* on color pattern) having apparently smaller scales. An attempt was made to express and analyze this fact.

Map of Colombian and Venezuelan localities for *Gonatodes albogularis*.

We resorted therefore to scale counts: (a) across the chest, (b) along the postero-ventral margin of the thigh, and (c) longitudinally, between arm level and vent.

The last character was ultimately chosen because of its extremely good reproducibility and wide numerical range. This count was made by sticking a pin on the line connecting the fore margin of the arms and counting the scales along the midline, from the point to the vent. In what follows, this character will be referred to simply as "ventral scales" or "ventral counts."

Ventral scales: the larger homogeneous samples (Tables 2 to 4).

The largest sample (19 males, 30 females) from a single locality showing only one color pattern is that from Sabanalarga, where only decided *fuscus* occur. It is easy to see that the distribution is symmetrical, the coefficient of variation is rather satisfactory, and there are no significant sexual differences. which the name *notatus* is available.

The second largest sample, also from a *fuscus* area, is that from Quibdó (9 males and 3 females). The male distribution is again symmetrical, variation moderate, and there are no indications of sexual differences.

The only sizeable sample of pure *albogularis* is that from Cucuta (9 males and 6 females). The females are more variable, but the means do not differ significantly.

Comparing these three samples it is seen that the two *fuscus* series agree perfectly, while that of *albogularis* has lower counts; there is no overlap and statistical tests are unnecessary.

It becomes thus logical to continue the study by analyzing the samples in which both color patterns appear mixed, and then the distribution of the character in the remainder of the range.

The mixed samples (Tables 2 and 3).

The only sample showing both color patterns and having numbers sufficient for statistical analysis is that from Honda (5 *albogularis* males, 6 *fuscus* males and 15 females).

There is a significant difference between the two male types, but the respective values are *opposite* to those seen in the previous comparison: the *albogularis* scale counts are higher. The females are intermediate and do not differ significantly from either male series.

The other mixed sample (Merida) is very small, and the counts indicate no differences, either sexual or between patterns. In general it agrees with the Cucuta series, which is rather

reasonable, as the specimens here determined as *fuscus* are very light-throated when compared to western Colombian examples.

Ventral scales: the general pattern.

Adding to the above data a survey of the small samples (Table 4 and map), it is quite obvious that extreme low counts are found in Cucuta and Merida, intermediate ones in Honda and San Gil, and uniformly high ones elsewhere. No sexual differences are apparent.

Correlation of the color and squamation characters.

Combining now the data on geographical differentiation of color patterns and of ventral counts, we see that: (1) all the pure *fuscus* samples have high counts; (2) one pure (Cucuta) and one mixed (Merida) *albogularis* sample have extreme low counts; (3) one small pure (San Gil) and one mixed (Honda) *albogularis* sample have intermediate values.

Thus, it must be said that the distributions of the two characters do not agree perfectly, yet the agreement is close enough. There is a core of white-throated, low-count animals, separated from their dark-throated, high-count fellows by a region where both characters intergrade independently. This is, in our view, compatible with the hypothesis of two subspecies; in fact, we believe this hypothesis to be the most probable. The fact that in the Honda series the association between color pattern and scale count changes sign is a further element in favor of the idea, as it would be hard to explain this on any other grounds than those of interaction between independently adaptive characters.

MATERIAL FROM OTHER PARTS OF SOUTH AMERICA

Specimens assignable to this complex are known from a few localities in South America in addition to those from which we have analyzed the above material.

Hummelinck (1940, pp. 73-74) has reported small series from the Colombian peninsula of La Goajira and from Aruba and Curaçao as *Gonatodes albogularis* and from Tortuga and Orchila as "*Gonatodes* spec. (? *albogularis* cff.)." From Curaçao Stejneger (1917) and following him Burt and Burt (1931) have already reported *albogularis*. Roze (1956) has recorded a member of the complex, not more precisely identified, from Gran Roque.

Of this material we have seen only the seven specimens, including one male, discussed by Stejneger from Curaçao. On both color and ventral counts they are *albogularis*.

Also available is a series from Gorgona Island, MCZ 6994, 7283 (12 specimens) — very poorly preserved but clearly *fuscus* in coloration and high in ventral counts.

We have not included these specimens in our discussion above. The material on these peripheral populations is in no sense adequate and it does not in any case alter the fundamental picture we have outlined for the Colombian populations. The only problem on which these peripheral populations shed any light is that of the total range of the species. They appear to imply — as the evidence now stands — a thinning out of the species toward the east in the regions where other, perhaps competing, species of the genus exist.

JAMAICAN AND HISPANIOLAN *GONATODES*

Hispaniolan adult males closely resemble Colombian *albogularis*, with two differences: (1) a prehumeral spot, dark blue with irregular bright white center — quite conspicuous in preserved specimens (this spot is not quite an ocellus, but is almost so); (2) the white throat, though mostly a dead white, like *albogularis*, often has a few isolated scales darkly pigmented or there may be a more general weak and obscure mottling.

Our Jamaican sample is very similar to the Hispaniolan. It suggests that specimens from this island might have a little more white in the spot, but this is, at best, a very subtle difference which we choose to disregard at this time. We consider Jamaican and Hispaniolan *Gonatodes* to represent the same taxon, for which the name *notatus* is available.

The scale counts (Tables 2 and 3) show absence of sexual differences in the two samples, and perfect agreement between them. The means are significantly higher than that of the Cucuta sample.

Thus, not only in color, but also in scale counts, *notatus* is closer to *albogularis* than to *fuscus*, but is clearly a distinct form.

CUBAN AND CENTRAL AMERICAN *FUSCUS*

The Central American populations belonging to the present complex are to all appearances identical with the Colombian populations we call *fuscus*. So also are the few Cuban specimens

available. The ventral counts of the few Cuban specimens are also high, higher indeed than the few Nicaraguan specimens counted for comparison.

NOMENCLATURE

The name *fuscus* Hallowell 1885 (type locality: Nicaragua) presents no difficulty, being clearly linked to Central American specimens of undisputed status. Pending study of differentiation between South and Central American material, it can be used provisionally for the Colombian darker-throated, smaller-scaled form. *Notatus* Reinhardt and Lütken 1863 (type locality, Acquin, Haiti) is likewise applicable to the well-documented Hispaniolan population.

A difficulty exists, however, with regard to the name *albogularis* Duméril and Bibron 1836, the oldest and, consequently, the one which must be given to the species. The locality of the type is said by Duméril and Bibron (1836:417) to be Martinique, Plée collector. The form has not been collected again in the island, and Barbour and Ramsden (1919) have cast doubt on this and other similar localities (in many cases with undoubted justice). Collecting in Martinique, however, has not been intensive enough to give certainty to the hypothesis that the species does not occur there, especially when the possibilities of human transport are considered.

On the other hand, the original description is very clear. The relevant points are (*loc. cit.*: 416): "Nous avons donné à ce Gymnodactyle la qualification d'*Albogularis* parce qu'en effect le dessous de la tête, et même celui du cou, offre un blanc extrêmement pur. Cette couleur se montre aussi sur le bas-ventre, sous les cuisses et la queue. Un noir profond colore les flancs et les parties latérales du corps. Toutes les régions supérieures de l'animal présentant une teinte ardoise. La poitrine est d'un gris blanchâtre."

This description applies very well to what has been called, by previous authors and by ourselves, *albogularis,* and to no other form. It is, therefore, unfortunate that Duméril and Bibron, under the heading "Patrie" (*loc. cit.*) say that the form occurs also in Cuba, from which place they had seen several specimens collected by Ramon de la Sagra.

Thanks to the generosity of M. Jean Guibe we have seen the three specimens (Paris No. 1776) now labelled as cotypes of *albogularis.* All three are said to be from Martinique. Two are

males with the dead-white throat of *albogularis* as we have interpreted it; the single female is not distinctive. The ventral counts (♂ ♂ 43, 46; ♀ 39) fall well within the limits of the Colombian specimens we have called *albogularis*.

Thus, though color in life, or some aspect of morphology that we have neglected, or a statistical difference in scale counts may just possibly distinguish an authentic Martinique population, it is certainly at the moment best to ignore the problems raised by the alleged provenance of the types and continue to apply the name *albogularis* as we have done throughout this paper.

COLOR IN LIFE

It is obvious that among the data which a final taxonomic arrangement of the *albogularis* complex must utilize will be color in life. Some data of this sort are available, but not consistently available. In particular it is not at hand for critical series and regions. As taxonomic evidence it has another defect: it is quite unstandardized and presents the rather casual observations of diverse observers, none of whom had any way of determining what might be significant in their observations. Ideally the living animals should be compared side by side and in the same state of health, breeding condition, etc.; such an ideal situation is very remote.

Nevertheless, it may be useful to compare the few statements that exist, since these notes may, on the one hand, permit some confidence in the decisions made on the basis of preserved material and, on the other, indicate problems within or possible subdivision of the larger groupings we have suggested above. We have organized the random data according to the taxonomic units we have proposed above and we restrict ourselves to adult males.

Gonatodes albogularis albogularis

Colombia. Hermano Niceforo Maria has provided us with descriptions of live males from Cucuta, Colombia [letter of July 21, 1960]: "Head and throat bright yellow; between the eyes and backwards from the eyes on to the nape the color is yellow mixed with gray. There is a pale blue black-edged vertical line in front of the forelimbs; a broad black band on each side of the forelimbs, the lower part of which as well as the lower surface of the thighs is white." Since the observation of a

blue vertical line in front of the shoulder suggested *notatus* we asked for further information on this point. In a letter of November 1, 1960, Hno. Niceforo Maria generously gave the following information: "Eleven male and seven female live specimens of *Gonatodes albogularis* from Cucuta are my recent capture. None has a white mark outlined by black in front of the shoulder. One male has a pallid coloration and shows a pale ashy blue mark in front of the shoulder."

Gonatodes albogularis fuscus

Central America. Field notes (paraphrased) by Thomas Savage for specimens collected in El Salvador (MCZ 57090-97 from Usulutan, Santa Maria) [the specimens are described after two hours in formalin]: "Gular area with three yellow lines, the two lateral curving up toward the eye; area between lines orange-yellow, tending more toward yellow in some, in all some places are distinct orange, even more orange in life. A blue area at the edge of mouth extending under eye along upper jaw towards snout. Head usually with a copper-colored hood, contrasting sharply with the back which is deep blue-black to black with a beady surface of black and blue vermiculations."

Costa Rica. Taylor (1956) has described color in life of Costa Rican specimens: "Head generally orange-brown to orange, with black spots below eye and mouth angle, body bluish black; tail on top and sides similar except tip which is dirty-flesh-white. Undersurface somewhat magenta. Chin and throat orange-red with a median yellow dividing line anteriorly and with traces of darker and lighter olive-yellow parallel lines; belly blackish with the specialized escutcheon scales dirty flesh; sides of neck somewhat olive."

Cuba. Stejneger (1917) gives color from a color sketch by a Mr. J. H. Riley made in 1900 from a living Habana specimen: "The male is of a bluish-black with head and neck of bright ochraceous yellow. There is a distinct sky-blue narrow line on the labials under the eye, a small spot of the same color above the ear and a crimson spot on the side of the neck on the yellow where it joins the black body color."

Barbour and Ramsden (1919) give the following description of live Cuban specimens (exact locality not specified): "Iris neutral gray; head ochraceous yellow turning to orange red below; neck same color as head, with a narrow dark brown median line extending to base of skull. Narrow pale cerulean

blue line on labials extending beyond opening of mouth. A small cerulean blue spot, formed by four scales, above the ear (this is not always present). Another cerulean blue line on shoulder where the ochraceous area meets the body color. Body above slate blue sprinkled with ochraceous scales. Tail velvety black for three-fourths of its length, turning to gray until the last quarter inch, which is white. Feet pale snake-gray.''

Gonatodes albogularis notatus

Haiti. Notes were made by Sarita Van Vleck for P. S. Humphrey for specimens collected on Gonave Island, Haiti: ''Throat brilliant yellow-orange. Venter green buff. Tail pale yellow green. Top of head greenish orange (in another specimen brilliant yellow-orange). Dorsum greenish brown. Lips in front of eye black and white. Scales between eye and shoulder patch sky-blue. *Shoulder patch white with black border.*''

Jamaica. Chapman Grant (1940) has elaborately described the Jamaican animals (the italics are ours): ''Throat and top of head beautiful burnt orange; throat marbled in darker and lighter burnt orange; labials and cheeks gunmetal blue; *vertical white mark at shoulder followed by black*; back olive; chest gray, belly white; a steel-blue stripe from groin forward halfway to armpit on each side; an incomplete dark collar separates yellow throat and gray chest.''

TAXONOMIC CONCLUSIONS

As a summary of the present stage of the investigation, the following points may be made:

It appears that two geographical races of the same species of *Gonatodes* occur in northwestern South America. At present they may be known as *Gonatodes a. albogularis* and *G. a. fuscus,* although (1) complete evidence is not yet available, (2) the name *albogularis* may turn out to apply to specimens from Martinique rather than to continental populations, and (3) the western Colombian populations may eventually be proved different from Central American *fuscus* proper. These reservations lead us to stress the Jamaican and Hispaniolan angles of the problem in the title of the present paper. However, we believe that the present scheme may be accepted as a working hypothesis and that, furthermore, it affords sufficient basis for the solution of the insular problem.

It is clear that the closest relationships of the Jamaican and Hispaniolan populations which, together, constitute *notatus*, lie with what we are calling *a. albogularis*. Whether the Antillean form should be considered as a race of *albogularis* or a separate speeies depends entirely on one's general attitude towards insular forms. We believe that, in spite of the obvious absence of an intergradation belt, relationship should be stressed by the application of the trinominal nomenclature, and consequently that the name *Gonatodes albogularis notatus* should be given to the Jamaican and Hispaniolan members of the genus. The presence of some South American *albogularis* with a blue (not white) mark in front of the shoulder reinforces our preference for subspecific allocation.

This primarily nomenclatorial conclusion should not obscure the interesting biological problems that are presented by this complex. There is much that deserves more complete investigation. The ecology of *fuscus* and *albogularis* both in the areas of unmixed and mixed populations calls for study. The significance to the animals themselves of the rather subtle difference in male coloration still needs to be discovered. Geographic variation in scale counts and in color in life *within* the major populations may be as interesting as in the zone of contact.

SPECIMENS EXAMINED[1]

Gonatodes albogularis albogularis. **"Martinique"**: Paris 1776 (3) cotypes; **Curacao**: USNM 13859 (7); **Colombia**: Cucuta, ILS 72a-h, 73a-e, MCZ 64322-25.

Gonatodes albogularis albogularis × *fuscus.* **Colombia**: Honda, ILS 68a-d, 75a-c, MCZ 19214-18, AMNH 27469-92; San Gil, ILS 71a-b, MCZ 36878-80, 64327-29; **Venezuela**: Merida, AMNH 5283, 13520-23.

Gonatodes albogularis fuscus. **Colombia**: Barranquilla, ILS 66a-b; Casabe, ILS 74a-c; Espinal, ILS 70a-d; Florencia, MCZ 64326; Fort San Felipe, AMNH 73535; Gualanday, MCZ 46434; Medellin, AMNH 38339, 38756-57, 38760-62, 46460-69; Puerto Salgar, ILS 67a-c, MCZ 64330-31; Quibdó, ILS 65a-c, AMNH 18231, 18247-48, 18250-56; Rio Frio, MCZ 25986-91; Sabanalarga,

[1] The following are the abbreviations for the several institutions, including the Museum of Comparative Zoology (MCZ), which furnished specimens for study: AMNH — American Museum of Natural History, New York; ILS — Instituto de La Salle, Bogota; UMMZ — University of Michigan Museum of Zoology, Ann Arbor; USNM — United States National Museum, Washington; YPM — Yale Peabody Museum, New Haven.

ILS 69a-b, AMNH 19900-21, 19925-39, 19941, 19943-45, 19947, 19950-55, 38673-74, 38759; Tambo, AMNH 18257; **Cuba**: Guantanamo, MCZ 8527-28, 14014-15, 60981; Havana, MCZ 7922; Santiago, MCZ 6918, 7284.

Gonatodes albogularis notatus. **Haiti**: Gonave, MCZ 25424, 61044-49, YPM 3063-86; Port-au Prince, MCZ 59471-2; Jamaica: Kingston, MCZ 7339 (3), 45019-24, UMMZ 85863 (5), 85864 (6), 85865 (3).

REFERENCES CITED

Barbour, T. and C. T. Ramsden

1919. The herpetology of Cuba. Mem. Mus. Comp. Zool. **47**: 71-213.

Burt, C. E. and M. D. Burt

1931. South American lizards in the collection of the United States National Museum. Proc. U. S. Nat. Mus. **78**: 1-52.

Cochran, D.

1941. The herpetology of Hispaniola. Bull. U. S. Nat. Mus. **177**: 1-398.

Duméril, A. M. C. and G. Bibron

1836. Erpétologie générale ou histoire naturelle complète des reptiles. Paris, vol. **3**: i-iv + 1-517.

Grant, Chapman

1940. II. The Reptiles, *in* The Herpetology of Jamaica. Bull. Inst. Jamaica. Sci. Ser. No. **1**: 61-148.

Hummelinck, P. W.

1940. A survey of the mammals, lizards and mollusks. Studies on the fauna of Curaçao, Aruba, Bonaire and the Venezuelan islands **1**: 59-108.

Roze, J.

1956. La herpetofauna de los islas Los Roques y la Orchila. *In* El Archipelago de Los Roques y La Orchila. Caracas, Venezuela. Pp. 79-86.

Stejneger, L.

1917. Cuban amphibians and reptiles collected for the United States National Museum from 1899 to 1902. Proc. U. S. Nat. Mus. **53**: 259-291.

Taylor, E. H.

1956. A review of the lizards of Costa Rica. Univ. Kansas Sci. Bull. **38**: 1-322.

TABLE 1

Incidence of *albogularis* and *fuscus* adult male color patterns in the samples studied.

Sample	*albogularis*	*fuscus*
Cucuta	9	—
San Gil	3	—
Merida	1	2
Honda	5	6
Rio Frio	—	2
Barranquilla	—	2
Puerto Salgar	—	3
Gualanday	—	1
Espinal	—	2
Sabanalarga	—	18
Medellin	—	4
Casabe	—	1
Quibdó	—	9
Florencia	—	1

TABLE 2

Distribution of frequencies of the number of ventral scales in the larger samples. Sexes and color patterns separate.

Ventrals	Cucuta ♂	Cucuta ♀	Honda[1] ♂a	Honda[1] ♂f	Honda[1] ♀	S'larga ♂	S'larga ♀	Quibdó ♂	Quibdó ♀	Hispaniola ♂	Hispaniola ♀	Jamaica ♂	Jamaica ♀
40		1											
41		1											
42	1	1		1						1		1	1
43	1	1		—						1	1	—	—
44	4	—		—						2	3	2	1
45	2	—		—						1	5	1	1
46	—	2		2	1					5	5	1	1
47	1			—	1					6	2	—	2
48				—	2			2		2	3	1	—
49			1	1	4			1		2	2	1	—
50			—	1	1	1	2	—	1	1	3		1
51			—	1	2	—	1	—	1	1	1		
52			2		—	5	9	—	1				
53			1		1	2	3	—					
54			1		2	3	4	1					
55					—	4	4	4					
56					—	—	3	—					
57					1	3	2	1					
58						—	2						
59						1	—						

[1] a, *albogularis*; f, *fuscus*.

TABLE 3

Description of the distribution of frequencies of the number of ventral scales in the larger samples[1]

Sample	N	R	M	s	V
Cucuta ♂	9	42-47	44.2 ± 0.46	1.39	3.1
♀	6	40-46	43.0 ± 1.05	2.58	6.0
♂ ♀	15	40-47	43.7 ± 0.50	1.94	4.4
Honda ♂ a[2]	5	49-54	52.0 ± 0.84	1.87	3.6
♂ f	6	42-51	47.3 ± 1.23	3.01	6.4
♀	15	46-57	50.2 ± 0.78	3.00	6.0
Sabanalarga ♂	19	50-59	54.1 ± 0.52	2.28	4.2
♀	30	50-58	53.7 ± 0.47	2.23	4.2
♂ ♀	49	50-59	53.9 ± 0.32	2.23	4.1
Quibdó ♂	9	48-57	52.9 ± 1.16	3.50	6.6
♀	3	51-53	51.0 ± 0.58	1.00	2.0
♂ ♀	12	48-57	52.4 ± 0.86	2.98	5.7
Hispaniola ♂	22	42-51	46.6 ± 0.46	2.17	4.6
♀	25	43-51	46.7 ± 0.43	2.14	4.6
♂ ♀	47	42-51	46.6 ± 0.32	2.18	4.7
Jamaica ♂	7	42-49	45.4 ± 0.92	2.44	5.4
♀	7	42-50	45.9 ± 0.96	2.54	5.5
♂ ♀	14	42-50	45.6 ± 0.64	2.40	5.2

[1] N, number of specimens in the sample; R, observed range; M, mean, plus or minus its standard deviation; s, standard deviation of sample; V, coefficient of variation.

[2] a, *albogularis*; f, *fuscus*.

TABLE 4

Distribution of frequencies of the number of ventral scales in the samples studied (sexes combined)

Ventrals	Sta. Marta	Barranquilla	San Felipe	Merida	Cucuta	San Gil	Sabanalarga	Pto. Salgar	Honda	Espinal	Medellin	Gualanday	Casabe	Quibdó	Pto. Asis	Florencia	Hispaniola	Jamaica
40					1													
41					1													
42					2				1								1	2
43					2				—								2	—
44				2	4				—								5	3
45				1	2				—								6	2
46				1	2				3								10	2
47				—	1				1				1				8	2
48				1		1			2				—	2			5	1
49						1			6			1	1	1			4	1
50		2				—	3	1	2			—	1	1		1	4	1
51						3	1	—	3	2	2	1	—	1		1	2	
52						—	14	1	2	1	3		—	1				
53	1					1	5	—	2	1	2	1	1	—	1			
54	—					1	7	—	3		1		—	1				
55	1		1			1	8	—	—		1		—	4				
56	1						3	2	—		1		1	—				
57	1						5	—	1		—			1				
58	1						2	—			—							
59							1	—			1							
60								—										
61								1										

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